THE AGE OF MAMMALS

HENRY FAIRFIELD OSBORN

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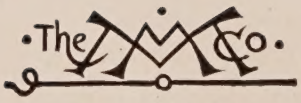

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THE AGE OF MAMMALS

IN

EUROPE, ASIA

AND NORTH AMERICA

BY

HENRY FAIRFIELD OSBORN

LL.D. (TRINITY, PRINCETON, COLUMBIA), HON. D.SC. (CAMBRIDGE)

VERTEBRATE PALÆONTOLOGIST OF THE UNITED STATES GEOLOGICAL SURVEY, DACOSTA PROFESSOR OF ZOÖLOGY IN COLUMBIA UNIVERSITY, CURATOR OF VERTEBRATE PALÆONTOLOGY IN THE AMERICAN MUSEUM OF NATURAL HISTORY

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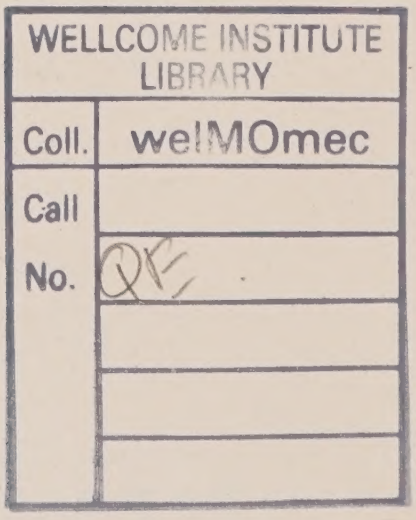

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TO MY BRITISH TEACHERS

THOMAS HENRY HUXLEY

AND

FRANCIS MAITLAND BALFOUR

THIS COMPARATIVE STUDY OF CÆNOZOIC MAMMALS
IN THE OLD AND NEW WORLDS

IS DEDICATED

PREFACE

To the memory of Huxley as my chief teacher in comparative anatomy, as well as to that of Balfour, my first teacher in embryology, I have dedicated this work. Huxley set forth the logic of Darwin as applied to palæontology; Balfour's genius was beyond imitation, but his pupils may follow the example of his ardent enthusiasm and his genial way of living the life of science.

Only a few men of the last century had the gift of speaking in clear language both to the learned and unlearned, and the greatest of these was Huxley. To write both for the man of one's own profession and for the layman, to be accurate and abreast of the specialist who knows as much or more of a subject than you do, while intelligible to the non-specialist — there is the difficulty. Many times have I thought to myself in the course of the preparation of these and similar lectures how simple it would be to address either audience separately. Yet I consider it fortunate that both are with us, because I share Huxley's confidence in addressing those who are willing to do a little serious thinking in order to enjoy the vast vistas of interesting truth which come as the reward of effort. I share also his conviction that it is the duty of the man of science to devote a certain part of his time, however absorbed in research he may be, to an honest attempt to scatter scientific truth. Although I may not claim that any parts of this volume are light reading, I have endeavored both to hold the attention of those who are already within the charmed temples of palæontology and to attract new votaries to its shrines. It should, however, be clearly understood that considerable sections of this work are purely documentary and may be passed over rapidly by the general reader.

Time and place are the main theme of this work rather than descent, which has been the main theme of all previous general treatises on the Cænozoic mammals; it is a study of the sources or birthplaces of the several kinds of mammals, of their competitions, migrations, and extinctions, and of the times and places of the occurrence of these great events in the world's history. To set forth this history in all its grandeur, it is interesting to consider the question of past environments, such as the past geography (palæogeography) of the earth, the changes in climate and in the earth's surface which conditioned the evolution of plant life (palæobotany) as the primary source of food supply for the mammals. Thus geology, geography, botany, and climate are treated as leading to a clear understanding of each of the successive groups and movements of mammalian life.

In a way this work marks the completion of a special line of study

which I began in 1898 and have been pursuing at intervals for eleven years, namely, the comparison of the new and old world life.

It is thus an exposition and explanation of two presidential addresses of mine delivered before the New York Academy of Sciences in February, 1899 and 1900, entitled "Correlation between Tertiary Mammal Horizons of Europe and America," also of a paper published recently by the United States Geological Survey, entitled "Cenozoic Mammal Horizons of Western North America." In the Introduction I have drawn freely on several popular addresses of mine, "The Rise of the Mammalia in North America" (1893), "Ten Years' Progress in the Mammalian Palæontology of North America" (1905), "The Present Problems of Palæontology" (1905), and, finally, "Palæontology," an article prepared for the forthcoming edition of the *Encyclopedia Britannica.*

The stimulus to put these studies into the present collected form was given by the generous foundation of the Harris Lectureship in Northwestern University by Mr. Norman Waite Harris in 1906. As originally delivered in December, 1908, to the students of that institution, the lectures were in general popular form. It has required a year to verify and expand them, so that the volume is practically of date December 31, 1909. The oral style appropriate to the lecture has given way necessarily to the written style; there is a greater fullness and I trust a greater clearness.

In gathering the materials for the preparation of these addresses and of this volume, my foremost acknowledgments are due to the profound and accurate researches of my friend, Professor Charles Depéret of the University of Lyons, as well as of my former student and present colleague in the American Museum of Natural History, Dr. William Diller Matthew. The very precise data which they have brought together, coupled with my own researches and observations on the mammals of the Old and New Worlds, have furnished the chief material for the broad comparisons and generalizations which I have attempted to make. I have also reviewed the general literature of the subject, and I desire to acknowledge the aid of my former student and present research assistant, Mrs. Johanna Kroeber Mosenthal, who has been intrusted with a large part of the reading, translation, and collation of facts derived from the foreign and American sources.

The reader will observe that the collections in the American Museum of Natural History as well as our observations in the field are very largely drawn upon. These have been gathered and planned during the past twenty years under my direction, and the fullest acknowledgments are due to the able and energetic explorers who have helped to bring these rare treasures of the past together, especially to Dr. J. L. Wortman, Dr. W. D. Matthew, Mr. J. W. Gidley, Mr. O. A. Peterson, Mr. Walter Granger, Mr. Barnum Brown, and Mr. Albert Thomson. The necessity for great precision in field records, especially for recording the exact levels on which specimens are found, I have impressed constantly upon the minds of these explorers. Such precise records have important bearing on the question of time as well as

of evolution; they were omitted in the pioneer work of Leidy, Marsh, and Cope. This precision in America, coupled with the precision especially of Professor Depéret's records and observations in France, has rendered possible the present comparison between the New and Old Worlds. Large collections have been secured also by the museums of Princeton University and the University of California, by the Carnegie Museum of Pittsburgh, the Field Museum of Natural History of Chicago; and some few additions have been made in recent years to the famous collection brought together by Professor Marsh in Yale University. The equally famous collection of Cope is now the property of the American Museum of Natural History.

The space and time distribution of the mammal life of Europe as set forth in Depéret's articles in the *Comptes rendus*, I have brought together in visual form in a new series of maps.

The American records, sections, and maps are drawn from those brought together in my recent bulletin, "Cenozoic Mammal Horizons of Western North America," together with some additions from my observations in Africa and from the very latest work in Wyoming. I am here indebted especially to the coöperation of Mr. Granger. The United States Geological Survey has given permission to reproduce many of the illustrations from my bulletin.

The reader who finds it difficult to picture the rare and ancient forms of mammals has to thank that gifted artist of the life of the extinct world, Mr. Charles R. Knight, for the series of restorations drawn under my personal direction, which are brought together for the first time in this volume. It is always to be understood that such restorations represent hypotheses merely or approximations to the truth. We know little or nothing about the color markings of these extinct forms, and even the attempt to outline the proportions of the limbs and body is somewhat hazardous; yet these representations serve, in connection with photographs of the skeletons, to give us a sense of the general size and proportion, and to assemble before the eye such inferences as to the homes and habits of the animals as can be deduced from their skeletons, especially from the teeth and feet, and from the kind of rock in which their remains have been discovered.

Mrs. L. M. Sterling has prepared many of the anatomical and geological illustrations with artistic fidelity. Mr. Aleth Biorn and Mrs. Mosenthal have prepared the Depéret series of maps. Mr. Erwin S. Christman has contributed several drawings. The field photographs are chiefly the work of Mr. Albert Thomson and other members of our field parties. The photographs of skeletons are part of the remarkable series executed by Mr. A. E. Anderson. I am indebted to many workers in other institutions for generous assistance. In the palæobotanic work I have enjoyed the assistance of Miss Elsbeth Kroeber, also of Messrs. F. A. Knowlton, A. A. Hollick, and T. D. A. Cockerell.

The entire text has been studied by Dr. W. D. Matthew and Dr. W. K. Gregory, to whom I am indebted for many valuable criticisms and suggestions.

A liberal appropriation by the trustees of the American Museum of Natural History has facilitated the large amount of special study, which has been devoted to the preparation and illustration of this work. I have also recently been transferred from a teaching to a research professorship in Columbia University.

Finally, the especial purpose of the work is to spread the knowledge of palæontology in the United States. It will be cause for regret if the extended information as to localities, here brought together for the first time, should lead to the hasty or untrained collection of fossils, or to the still more harmful ill-considered description of new species. All descriptions should be preceded by painstaking examination of previous types, and should be accompanied by figures and short, clear diagnoses. All type specimens should find their way into large central and accessible museums where they can be readily examined.

HENRY FAIRFIELD OSBORN.

American Museum of Natural History,
December 31, 1909.

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THE HARRIS LECTURES

DELIVERED AT NORTHWESTERN UNIVERSITY, DECEMBER, 1908

CHAPTER I — INTRODUCTION

HISTORY OF PALÆONTOLOGY — ENVIRONMENT — PAST AND PRESENT GEOGRAPHIC DISTRIBUTION OF MAMMALS

I. Philosophy of the Structure of Mammals

Rise of Palæontology

Palæontology is the zoölogy of the past. As a science it arose during the latter part of the eighteenth century in various parts of Europe with the first comparisons of the extinct with existing forms of life. Among the mammals such comparisons were instituted by Buffon and others; Cuvier subsequently formulated these into a complete system of study, and was thus the founder of vertebrate palæontology; he was also the pioneer in the art of restoration of the extinct forms of mammalian life and the conditions under which they lived.

Cuvier in his famous *Discours*[1] observed that naturalists recoiled from the difficulties which faced them because of the imperfections of fossils.

"Even if we should meet with the whole skeleton," he remarked, "we should have great difficulty in applying to it characteristics for the most part derived from the hair, color, and other marks which disappear before incrustation. It is uncommonly rare to find a fossil skeleton at all perfect; the bones are isolated, confusedly intermingled, most frequently broken, and reduced to fragments; this is all which our geologic layers furnish us, and is the sole resource of the naturalist. . . . Frightened at these difficulties, the majority of observers have passed lightly over the fossil bones of quadrupeds, classed them very vaguely after superficial resemblances, or have not even hazarded the giving of a name to them, so that this part of fossil history, the most important and instructive of all, is of all others the least cultivated."

"I do not pretend by this remark," continues Cuvier, "to detract from the observations of Camper or of Pallas, of Blumenbach, Sœmmering, Merk, Faujas, Rosenmüller, Home, and others; but their assembled labors which have been very useful to me and which I have cited elsewhere are only partial." [Footnote to French Edition, p. 47.]

Among these pioneers of mammalian palæontology in Europe to whom Cuvier refers were the vertebrate zoölogists and comparative anatomists

[1] Baron Georges Léopold Chrétien Frédéric Dagobert Cuvier, 1769–1832, Discours sur les Révolutions de la Surface du Globe; et sur les changemens qu'elles ont produits dans le règne animal. 4to. Paris, 1826.

Peter Simon Pallas, Pieter Camper, and Johann Friedrich Blumenbach. Pallas (1747–1811) in his great journey (1768–1774) through Siberia discovered the vast deposits of extinct mammoths and rhinoceroses. Camper (1722–1789) contrasted (1777) the Pleistocene and recent species of elephants; Cuvier (1799) published his memoir on the living and fossil elephants; and Blumenbach (1752–1840) separated (1803) the mammoth from the existing species of elephants as *Elephas primigenius*. In 1792 Kerr distinguished the American mastodon as *Elephas americanus*. In 1799 Thomas Jefferson (1743–1826) described the giant American Pleistocene sloth *Megalonyx*.[1]

The ancient life of the Atlantic border of North America was also becoming known through the pioneer work of Richard Harlan (1796–1843), Jeffries Wyman (1814–1874), and Joseph Leidy (1823-1891). The master works of Joseph Leidy began with the first fruits of western exploration in 1847, and extended through a series of grand memoirs, culminating in 1874. Leidy adhered strictly to Cuvier's exact descriptive methods, and while he was at heart an evolutionist and recognized clearly the genetic relationships of the horses and other groups, he never indulged in speculation.

Cuvier's Law of Correlation. — As a means of escaping the difficulties caused by the imperfections of fossils, Cuvier formulated and announced his famous 'law of correlation.' He reposed in this law a buoyant confidence which subsequent experience has shown to have been largely misplaced. He replied to the critics of the new science of palæontology, who deplored the imperfect nature of fossils, that the comparative anatomist does not require the entire animal, because certain laws of invariable association enable him to predict from a single part the structure of other parts. Thus, he observed, we are establishing supposititious laws which become almost as certain as the laws of reasoning, so that now any one who sees the track of a cleft foot may conclude that the animal which left it is ruminant; and this assertion is as sure as any other in physics or morality. This footmark alone gives to the observer both the formation of the teeth, the shape of the jaws, the structure of the vertebræ, and the form of all the bones of the legs, thighs, shoulders, and even the frame of the animal which has passed. It is a more certain mark than all those of Zadig.[2]

None of the numerous and genuine scientific discoveries of the great Frenchman brought him such immediate prestige as did this famous law. In reference to it Balzac said at the time that Cuvier "rebuilt like Cadmus cities, from a tooth"; yet, although in part defended by Huxley,[3] there is more error than truth in this law as Cuvier conceived it, for there

[1] Jefferson, Thomas, A Memoir on the Discovery of Certain Bones of a Quadruped of the Clawed Kind in the Western Parts of Virginia. *Trans. Amer. Philos. Soc.*, Vol. IV, 1799, pp. 246–260.

[2] The above paragraph is a literal translation from Cuvier's Discours. See full title, p. 1.

[3] Huxley, On the Method of Palæontology. *Ann. Nat. Hist.*, Vol. XVIII, 1856. Scientific Memoirs, 1898, Vol. I, pp. 436–439.

never is, as he believed, any 'invariable association' between the various parts of mammals. This is because each part is adapted to the particular service which it has to perform for the animal as a whole, service which may be rendered in many different environments and on many different kinds of food. While the feet and limbs are becoming fitted to moving in the water, or on land, in trees or in flight through the air, the teeth at the same time may become fitted to one of many different kinds of food, to shrubs, grasses, bark, insects, or to other animals. Thus, while serving the whole, different parts of animals evolve separately and independently, and there have arisen consequently an almost unlimited number of combinations of foot, limb, skull, and tooth structure.[1] The simple reason why a law conceived by a special creationist is invalid is that while all parts of an animal conspire to make the animal as a whole adaptive, there is no fixed correlation either in the form of the parts or in the speed with which they evolve.

It is consequently impossible for the palæontologist to predict the entire structure of an unknown animal from one of its parts only, unless the part happens to belong to a type already very familiar. For example, if we found the fossil claw bone of the cat we would know that it belonged to a cat and would be able to restore the cat; but if we found a claw bearing only a general likeness to that of the cat it would be very unsafe to restore the cat. There are herbivorous quadrupeds (fam. Chalicotheriidæ) in which the claws remotely resemble those of the giant ground sloths and anteaters; it happened that one of these very claws (of the genus *Macrotherium*) was brought to Cuvier, and full of confidence in his law, but entirely deceived by the resemblance of the claw to that of one of the existing scaly anteaters (the pangolins of Africa and India), he termed the animal *Pangolin gigantesque*. Had he restored the animal according to his own 'law of correlation,' he would have pictured a giant anteater of a structure as wide as the poles from what we now know to be the actual form of the quadruped, *Macrotherium*, which in body, limbs, and teeth is a true herbivore remotely related to the odd-toed quadrupeds known as titanotheres.

Again, in direct opposition to Cuvier's law we find that certain American Eocene monkeys (*Notharctus*), in which the limbs are fitted to tree-living, or arboreal, habits, exhibit grinding teeth very similar to those of the ground-living Eocene horses (*Orohippus*), in which the limbs, on the contrary, are distinctly of the running, or cursorial, type. Because of their teeth these monkeys were at first thought to be hoofed animals. Thus teeth do not give us certain indications of the form of the hoofs, nor does the form of the hoof give certain indications of the form of the teeth.

Evolutionary law of correlation. — Yet despite this independent evolution of parts, every part does conspire to make the animal as a whole adap-

[1] See the Law of Adaptive Radiation, p. 22.

tive, so that there is always a true adaptive correlation, although not of invariable association of certain kinds of organs, as Cuvier conceived it. The law of correlation of tooth and foot structure may, therefore, be restated as follows:—

The feet, which are correlated chiefly with the limb and body structure, and the teeth, which are correlated chiefly with the skull and neck structure, diverge and evolve independently in adaptation to securing food and to eating food under different conditions of life and in different environments. Each part evolves directly to perform its own mechanical functions and purposes, yet in such a manner that each subserves all the other parts.[1]

Systematic Palæontology

After the splendid osteological investigations of Cuvier had revealed a new mammalian world of wonderful richness, his successors were bent upon multiplying the diversity of this extinct creation, that is, adding new species and genera, rather than on closely studying the osteology of the fossil forms or adding new working principles to the science. In France De Blainville was the one great generalizer up to the time of Gaudry. Thus both in France and America facts accumulated more rapidly than principles. Cuvier's chief contributions were to the Upper Eocene mammals, to a few Miocene forms, and to many Pleistocene forms. His successor, Henri Marie Ducrotay de Blainville (1778–1850), in his *Ostéographie des Mammifères*[2] (1839–1864) added to the knowledge of the Basal and Lower Eocene fauna of France. Croizet and Jobert[3] described (1828) the mammals of Perrier and Malbattu, Upper Pliocene. In the middle of the century Paul Gervais (1816–1879) published his *Zoologie et Paléontologie Françaises.*[4] In 1851 Edouard Lartet (1801–1870) published his *Notice sur la Colline de Sansan.*[5] Sansan is a rich Middle Miocene deposit discovered by Lartet in 1834, explored for many years, and finally monographed by Henri Filhol (1843–1907) in 1891.[6]

[1] Cf. pp. 192, 193, of Osborn, The Rise of the Mammalia in North America. *Amer. Jour. Sci.*, Nov. and Dec., 1893.

[2] Ducrotay de Blainville, Ostéographie ou Description Iconographique Comparée du Squelette et du Système Dentaire des Mammifères Récents et Fossiles pour Servir de Base à la Zoologie et à la Géologie. Paris, 1839–1864.

[3] Croizet et Jobert, Recherches sur les Ossemens fossiles du Département du Puy-de-Dôme. Paris, 1828.

[4] Gervais, Zoologie et Paléontologie Françaises. Nouvelles Recherches sur les Animaux Vertébrés dont on Trouve les Ossements Enfouis dans le Sol de la France et sur leur Comparaison avec Espèces Propres aux Autres Régions du Globe. Paris, 1859.

[5] Lartet, Notice sur la Colline de Sansan, suivie d'une Récapitulation des Diverses Espèces d'Animaux Vertébrés Fossiles Trouvés soit a Sansan, soit dans d'Autres Gisements du Terrain Tertiaire Miocène dans le Bassin Sous-Pyrénéen. Auch, 1851.

[6] Filhol, Étude sur les Mammifères Fossiles de Sansan. *Ann. Sc. Géol.*, XXI, 1, Art. 1. Paris, 1891.

The still richer Lower Oligocene and Upper Eocene mammals of the phosphorites near Quercy, discovered in 1865 and noticed by various authors, were monographed by Filhol in 1877.[1]

The important Lower Oligocene mammals of Ronzon, discovered by Auguste Aymard, first reported in 1856, were fully and ably monographed by Filhol in 1881. The Upper Oligocene of the center of France (*l'Allier, Puy-de-Dôme, Haute-Loire*), successively described by Charles Depéret, Antoine Jacques Louis Jourdan (1788–1848), Gervais (1851), Nicolas Auguste Pomel (1853), was also finally monographed by Filhol in 1880.

It remained for Victor Lemoine (1837–1897) to describe the Basal Eocene mammalian fauna from Cernay near Rheims, discovered in 1873, and continuously explored up to the present time.

In the meantime in Germany the works of Georg August Goldfuss (1782–1848), Georg Friedrich von Jäger (1785–1866), and Christoph Gottfried Giebel (1820–1881, *Fauna der Vorwelt*, 1846, 1847) were followed by the more exhaustive publications of Johann Jakob Kaup (1803–1873), which covered the Upper Miocene mammals of the Mainz Basin (Eppelsheim near Worms). The gifted Christian Erich Hermann von Meyer (1801–1869) also described *Hipparion* and other mammals from Eppelsheim (1832). To Johann Andreas Wagner (1797–1861) we owe our first knowledge of the Upper Miocene fauna (1848–1857) of Pikermi, a wonderfully rich deposit which was finally monographed (1862) by Albert Gaudry (1827–1908). The Middle Miocene mammals of Württemberg were described (1870–1885) by Friedrich August Quenstedt (1809–1889) and Oscar Friedrich van Fraas (1824–1897).

The work of William Buckland (1784–1856) and John Phillipps (1800–1874) on the sparse Tertiary formations of Great Britain was followed by that of Richard Owen (1804–1892), which was finally summarized in his "A History of British Fossil Mammals and Birds" (1846), and "Contributions to the History of British Fossil Mammals" (1848), treating especially of the Upper Eocene of the Isle of Wight.

Darwin's Influence

A review of the two classic works[2] of Darwin (Charles Robert, 1809–1882), of 1839 and 1859, proves that he was the founder of modern palæontology. He applied to the living world the earth-forming principles of Hutton which had been grandly developed and expressed by Charles Lyell. The ideas of the descent of mammals and other applications of this law of similarity between the past and present history

[1] Filhol, Recherches sur les Phosphorites du Quercy. Paris, 1877.

[2] Narrative of the Surveying Voyages of His Majesty's Ships *Adventure* and *Beagle* between the years 1826 and 1836, Describing their Examination of the Southern Shores of South America and the *Beagle's* Circumnavigation of the Globe, published in 1839. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life, published in 1859.

of the earth, or uniformitarianism, had been struggling for expression in the writings of the French evolutionists Lamarck (Jean Baptiste Pierre Antoine de Monet de, 1744–1829) and Étienne Geoffroy St. Hilaire (1772–1844), as well as in the classifications of another great Frenchman, De Blainville. These ideas found in Darwin their first true interpretation, because the geological succession, the rise of mammals, their migrations, their extinctions, were all connected with the great central idea of divergent evolution from primordial forms. The impulse which Darwin gave to mammalian palæontology was immediate and unbounded, finding expression especially in the writings of Thomas Henry Huxley (1825–1895) in England, of Jean Albert Gaudry (1827–1908) in France, of Edward Drinker Cope (1840–1897) and Othniel Charles Marsh (1831–1899) in America.

The first fine exposition of the new spirit of the period as applied to extinct Mammalia is Gaudry's *Animaux Fossiles et Géologie de l'Attique* (1862), based on the Upper Miocene fauna of Pikermi near Athens. This work, to which we shall make many references, is full of genius. Especially noteworthy is Gaudry's discovery that mammals in their descent or phylogeny follow not one but many contemporaneous and parallel lines. In other words, Gaudry first enunciated the *polyphyletic law as applied to mammals*, but singularly his subsequent writings were not consistent with this law.

The remarkable memoirs of Vladīmir Onufrievīch Kowalevsky (1842–1883), published in 1873, are monuments of exact observation of the details of evolutionary change in the skull, teeth, and feet, and of the appreciation of Darwinism. In the most important of these memoirs, entitled *Versuch einer Natürlichen Classification der Fossilen Hufthiere* (1873), we find a model union of detailed inductive study with theory and working hypothesis. These works swept aside the dry traditional fossil lore which had been accumulating in France and Germany. They breathed the new spirit of recognition of the struggle for existence, of adaptation and descent.

Huxley's most vital contribution was his development of the *method of palæontology*, or the modes of examining and testing facts, of synthesis and analysis. These may now be studied in his collected memoirs.[1] His principles of analysis are complete except in his failure to realize the wonderful operation of the *law of analogy* in the repeated creation of similar forms from dissimilar ancestors.

All these writers attacked the problem of descent, and published preliminary phylogenies of such animals as the horse, rhinoceros, and elephant, which time has proved to be of only general value and not at all comparable to the exact descent series which were being established during the same period by invertebrate palæontologists, beginning with the

[1] Scientific Memoirs of Thomas Henry Huxley, 4 vols, London, 1898–1903.

memoirs of Wilhelm Heinrich Waagen in 1869. Phyletic or ancestral gaps began to be filled in a general way, however, especially through remarkable discoveries in North America by Leidy, Cope, and Marsh; and the ensuing phylogenies, or 'trees,' of animal descent gave enormous prestige to palæontology, as affording the most convincing proofs of evolution.

Primitive and progressive stages. — It was early (1870–1873) observed by Huxley, Cope, and others that Cuvier's broad belief in a universal law of perfection was erroneous, and they began to perceive the difference between persistent primitive types (Huxley) and progressive or advancing types. Darwin himself had anticipated that primitive or stem forms of the existing modernized or specialized kinds of animals would be discovered. The analytic steps by which from existing knowledge the stem form might be reconstructed before its discovery, were first fully and clearly described by Huxley in 1880,[1] namely, by separating all the specialized, or modern, characters of mammals from all the primitive, or original and simple characters, and by putting together the latter to compose an ancestral or stem form of mammal. Thus, more or less independently, Huxley, Kowalevsky, and Cope had ventured to picture what the ancestor of the hoofed mammals, or ungulates, would be like when discovered, namely, an animal whose chief characters would be grinding teeth with simple, rounded cusps, and feet with five separate and complete digits. This prophecy and restoration at first seemed to have been entirely realized and fulfilled in the discovery in northern Wyoming, in 1873, of a generalized hoofed mammal, to which Cope gave the name *Phenacodus*, although this mammal has since proved not to be directly ancestral to any form, but rather to stand for a type.

The reconstruction of primitive ancestral forms was so much more facile and enjoyable than the arduous labor of exploration and research that it naturally went to extremes. Here we are reminded of a critical saying of the late Professor von Gudden, the distinguished neurologist of Munich: "*Ein Steinchen der Wahrheit hat mehr Werth als ein grosser Schwindelbau.*" In palæontology the great "*Schwindelbau,*" literally "the false structure," is the phyletic tree, which adorns the end of many good as well as many superficial papers. Recently, because of their extremely brief existence, these phylogenies have fallen somewhat into disfavor, yet the present reaction against these trees does not seem to be altogether wise, for we must remember that they are among the working hypotheses of this science, which serve to express most clearly the author's meaning.

Precise and philosophical research. — The first twenty years after the publication of Darwin's "Origin" will always remain a golden era in the

[1] Huxley, On the Application of the Laws of Evolution to the Arrangement of the Vertebrata and more Particularly of the Mammalia. *Proç. Zoöl. Soc.*, London, 1880, pp. 649–662; Scientific Memoirs, Vol. IV, pp. 457–472.

history of mammalian palæontology, including the labors of those mentioned above as well as of the great Swiss palæontologist, Ludwig Rütimeyer (1825–1895). It was under the inspiration of the "Odontographie" [1] of Rütimeyer that Kowalevsky completed and published in 1873 his four remarkable memoirs upon the hoofed mammals. He wrote these four hundred and fifty quarto pages in three languages not his own, in French upon *Anchitherium* and the ancestors of the horses, in English on the Hyopotamidæ, in German upon other types of even-toed mammals, namely, *Gelocus*, *Anthracotherium*, and *Entelodon*,[2] including the first attempt at an arrangement of these great groups of mammals on the basis of the descent theory. It is to the everlasting renown of the veteran Rütimeyer and of Kowalevsky, unfortunately so soon deceased, that while their main inductions as to the descent of the mammals and even as to the structure of certain parts of mammals, such as the teeth, have suffered by the fullness of American discoveries, their methods of thought and still more their thorough methods of research have not been displaced. Kowalevsky's theory of the pedigree of the horses, like that of Huxley, was not the right one; Rütimeyer believed that the grinding teeth of hoofed mammals sprang from lophodont or crested forms, which also has been disproved. It is, nevertheless, the right system of thought which is most essential to progress; and better in the end wrong results which have been reached by right methods than right results reached haphazard by vicious methods. If a student to-day asks, "how shall I study palæontology," we can do no better than to direct him to the *Versuch einer Natürlichen Classification der Fossilen Hufthiere* of Kowalevsky, out of date in some of its facts, thoroughly modern in its method of approach to ancient nature. This work is a model union of the detailed study of form and function with theory and the working hypothesis. It regards the fossil not as a petrified skeleton, but as having belonged to a moving and feeding animal; every joint and facet has a meaning, each cusp a certain significance. Rising to the philosophy of the matter, it brings the mechanical perfection and adaptiveness of different types into relation with environment, with changes of herbage, with the introduction of grasses. In this survey of competition it speculates upon the causes of the rise, spread, and extinction of each animal group. In other words the fossil quadrupeds are treated *biologically* — so far as possible in the obscurity of the past. From such models and from our own experience we learn to feel free to abandon outworn traditions in the use of the tools of science, such as mere methods of description and classification, and to conserve a reasonable priority in nomenclature only.

[1] Rütimeyer, L., Beitrag zur Kenntniss der fossilen Pferde und zu einer vergleichenden Odontographie der Hufthiere im Allgemeinen. *Verh. naturf. Ges. Basel*, Vol. III, no. 4, 1863.

[2] Readers desiring to ascertain the zoölogical relations of these and other mammals mentioned in the text should consult the index and appendix.

New discoveries continually produce new conditions; there is nothing more obstructive than reverence for old ideas and systems which have outlived their usefulness. In observation the old motto seems to have been *de minimis non curat lex*, to the effect that one can afford to pass over the minute; at the present time we cannot be too exact in the observation of the minute. The vertebrate palæontologist must follow the precise methods long ago introduced by Waagen (1869) among the invertebrates. Every rudiment of a cusp on a tooth, or facet, or articulating surface on a bone has its value, not as a sign-post on which to hang a new species, but as suggestive of the dawn of some new character, or the instrument of some function or relationship; the old bird's-eye methods of comparison, which found no difference between the grinding teeth of a rhinoceros and of a lophiodon, are of no service when we are called upon to distinguish between many lines of ancient mammals crowding in among the ancestors of existing mammals. Such methods of precise observation we owe largely to the influence of Rütimeyer and Kowalevsky.

Influence of American Discovery

The first mammalian remains from the Badlands of the Great Plains of the West, east of the Rocky Mountains, consisted of fragments of the lower jaw of the enormous quadruped, later called *Titanotherium*, which was described by Dr. Hiram A. Prout of St. Louis in the *American Journal of Science* in 1846. We now know that this specimen was of Lower Oligocene Age. Travelers connected with the American Fur Company brought other specimens East in 1846 and 1847. In 1849 Dr. David Dale Owen and Dr. John Evans explored the "Mauvaises terres," and brought back collections which were first described in Owen's Geological Report of 1852. This attracted a great deal of attention, and led to the prolonged explorations of Ferdinand Vandeveer Hayden (1829–1887) and Fielding Bradford Meek (1817–1876) between 1853 and 1866 of the whole region of Nebraska and Dakota. The collections of mammalian remains, practically all of which were new to science, fell into the able hands of Dr. Joseph Leidy of Philadelphia. In 1852 he published his first volume, entitled "The Ancient Fauna of Nebraska," [1] and in 1869 appeared his great work "The Extinct Mammalian Fauna of Dakota and Nebraska," [2] which closed with a synopsis of all fossil mammalian remains of North America known at that time. This monumental work laid the broad foundations of modern study and must still be considered one of the greatest single contributions to the mammalian palæontology of North America.

[1] Leidy, The Ancient Fauna of Nebraska, or a Description of Remains of Extinct Mammalia and Chelonia. *Smithson. Contrib. to Knowl.*, Vol. VI, 1852.

[2] Leidy, J., The Extinct Mammalian Fauna of Dakota and Nebraska, including an Account of some Allied Forms from other Localities, together with a Synopsis of the Mammalian Remains of North America. Philadelphia, 1869.

Subsequent research has shown that, considering the great difficulties under which they labored, Hayden and Leidy formed a surprisingly accurate conception of the geologic or time succession of mammalian forms in Oligocene, Miocene, and Pliocene times. Hayden's explorations of 1869–1870 in the interior of the Rocky Mountain region led to the discovery of the Bridger deposits of Middle Eocene Age, the rich extinct mammalian life of which was monographed by Leidy in 1873.

The complete geologic succession of the vast ancient life of the American continent was destined to demonstrate the evolution law. The brief narrative of this succession, as known to-day, forms one of the chief subjects of the present volume. Between 1871 and 1873 Marsh and Cope took up the labors of Leidy in the exploration of the Rocky Mountain basins, rich in fossil life. The first ten years of their work not only modified our ideas of the descent of the mammals, but brought together data for a number of important generalizations: for Marsh's demonstration [1] that the size of the brain was an important factor in survival, that most small- and smooth-brained mammals early became extinct; for Cope's proof that the hoofed animals sprang from types with simple, five-toed feet, resting largely upon the sole, and with conic cusps on the grinding teeth. Finally between 1879 and 1883 came Cope's demonstration that the grinding teeth of most of the mammals had passed through a triangular form in the early Eocene period, in which three tubercles, or a tritubercular structure, is apparent.

Fig. 1. — Primitive stage in tooth development. Typical tritubercular, upper molar of the mesonychid creodont, *Triisodon* of the Basal Eocene, Puerco Formation. After Osborn, 1907.

Primitive and progressive forms of teeth. — This discovery by Cope [2] of primitive and widespread trituberculy in the molar or grinding teeth was a great step forward. We find in the previous descriptive works or odontographies of Cuvier and of Owen not even a suspicion of the existence of a common or primitive type of grinding tooth from which the highly specialized "cheek teeth" of the different mammals have evolved. At the present time we may compare the molars of the clawed and the hoofed mammals with each other because they sprang from a common tritubercular type, just as we compare the hand or foot of man, of the horse, the cat, because we know they sprang from a common five-fingered type. Nearly all kinds of mammals, hoofed quadrupeds, monkeys, carnivores, insectivores, rodents, marsupials, are found building up their grinding teeth on the basis of this primitive tritubercular ancestral form.[3] We thus have a key to the com-

[1] Marsh, O. C., Dinocerata. A Monograph of an Extinct Order of Gigantic Mammals. *U.S. Geol. Surv.*, Vol. X, Washington, 1884, p. 58 fol.; *see also* Marsh, '74 and '85 in Bibliography.

[2] Cope, E. D., On the Trituberculate Type of Molar Tooth in the Mammalia. *Pal. Bull.* no. 37, *Proc. Amer. Philos. Soc.*, Vol. XXI, Dec. 7, 1883, pp. 324–326.

[3] See Osborn, H. F., Evolution of Mammalian Molar Teeth, 8vo. New York, 1907.

parison of the molar teeth of nearly all mammals, and similar names can be given to the cusps in the upper and lower molar teeth respectively.

This tritubercular molar owed its survival to three features: (1) the original advantage of its triangular form as expressed in the term "trigonodont" proposed by Rütimeyer; (2) the possibility of free addition of

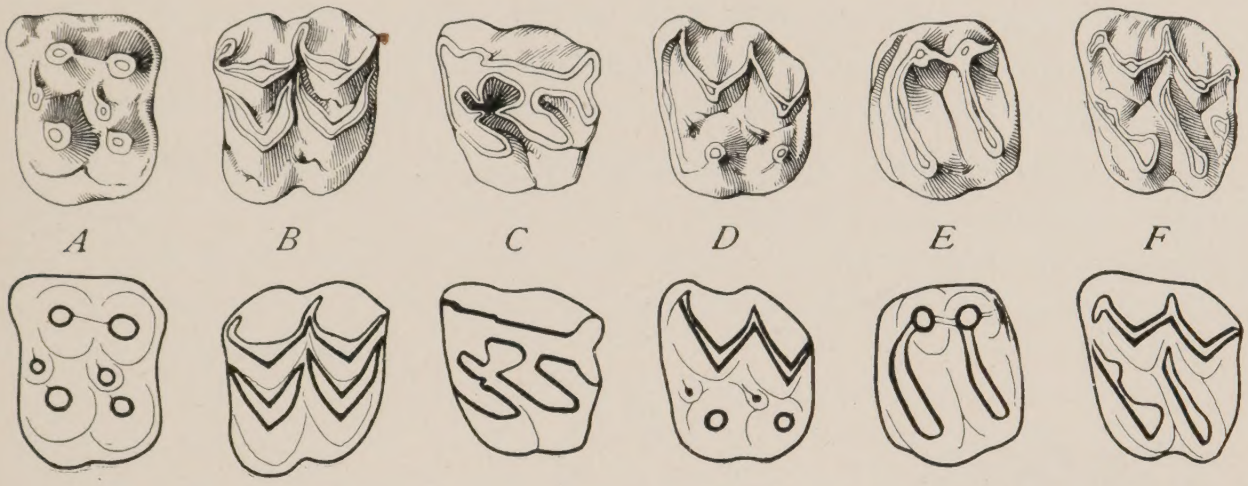


FIG. 2. — Types of superior molar or grinding teeth. *A.* Bunodont, all conic, *Hyracotherium*. *B.* Selenodont, all crescentic, *Protoceras*. *C.* Lophodont, all crested, *Rhinoceros*. *D.* Buno-selenodont, conic-crescentic, *Palæosyops*. *E.* Lopho-bunodont, crested-conic, *Tapirus*. *F.* Lopho-selenodont, crested-crescentic, *Anchitherium*.

new cusps as worked out in detail by Cope, Osborn, Scott, Wortman, Schlosser, and others; and (3) the wonderful independent modeling of these cusps either singly or in pairs into different forms, some remaining rounded, or bunoid, others becoming elongate, crested, or lophoid, others becoming crescentic or selenoid, as shown in the accompanying figures (Fig. 2).

Taking the Greek derivatives βουνός (hillock), λόφος (crest), σελήνη (moon, *i.e.* crescent), and joining them with the word ὀδοῦς (tooth), we have very simple names for the various types of teeth in which all the tubercles passed through the same form. These teeth may be either bunodont, lophodont, or selenodont. There is a marvelous, independent, adaptive evolution of each cusp; one cusp may remain rounded while its neighbors become crescentic, and we thus find compound patterns, which may be given the somewhat cacophonous terms "bunoselenodont," or in the case of the conic-crested form, "bunolophodont."

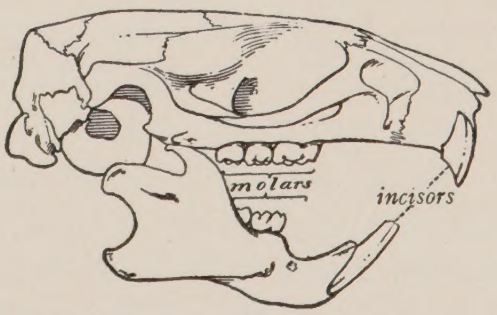


FIG. 3. — Skull of the rat, showing extreme diprotodonty of the upper and lower incisor teeth. After Matthew, 1905.

Diprotodonty, or the enlargement of a pair of cutting teeth, is an adaptation which arises frequently and independently in insectivores, rodents, monkeys, tillodonts, primitive edentates, and other orders. Sometimes it is the middle pair of incisor teeth, sometimes the second pair which is enlarged, while the surrounding teeth are reduced.

The enlarged teeth are often so similar as to be very misleading in regard to relationship or affinity.

As regards the elongation of the teeth the parallel with that of the feet is very close indeed, for we distinguish the following kinds of teeth:

BRACHYODONT, primitive short-crowned teeth, with simple roots and simple cusps, and usually with simple conic, crescentic, or crested cusps, as of the pig, deer, and mastodon.

HYPSODONT, elongate grinding teeth, as of the ox, horse, and elephant.

Just as the power of an herbivorous animal to move long distances or to take wide excursions in search of food or to move rapidly in escaping its enemies is brought about through changes in the number of digits, and in the form and proportions of the feet, so the power of an animal to live a long period of time and to assimilate the harder kinds of food is increased through changes of form and proportion in the teeth. The hypsodont horse attains over thirty years of age; the hypsodont elephant lives about a hundred years.

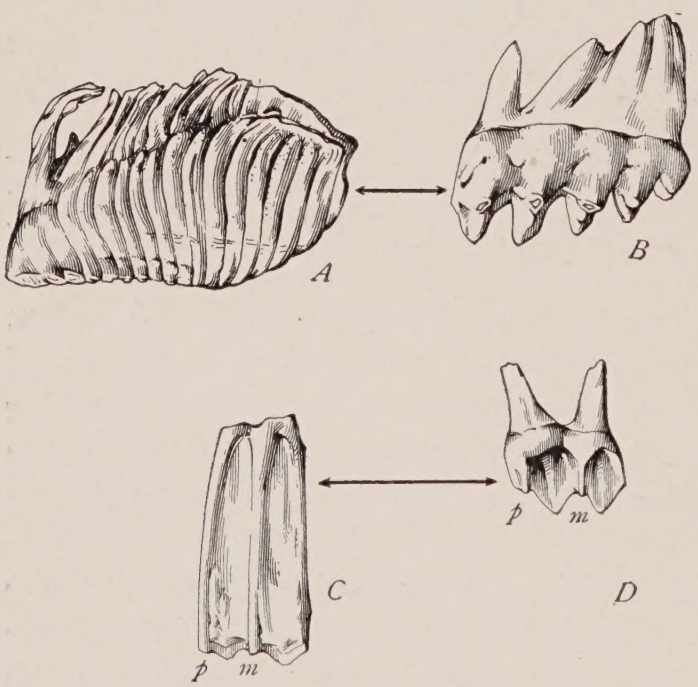


FIG. 4. — Tooth proportions, or brachyodonty and hypsodonty. *B*. Brachyodont, short-toothed, *Mastodon americanus*. *A*. Hypsodont, long-toothed, *Elephas meridionalis*. *D*. Brachyodont, short-toothed, *Anchitherium aurelianense*. *C*. Hypsodont, long-toothed, *Equus caballus*.

Elongate teeth may be far more highly perfected mechanically and have more complicated crowns, consisting of three different dental tissues of three degrees of density, namely, enamel, dentine, and cement, thus affording three degrees of resistance, and always presenting a rough or uneven grinding surface. The passage from short-crowned to long-crowned teeth also marks the passage from browsing forms, living on softer kinds of food, to the grazing forms, living on the harder kinds of food, as well as from more short-lived animals to more long-lived animals. Here again we see that the elongation of the teeth like the elongation of the feet is eminently adaptive. For example, where physiographic changes reduce the softer herbage and increase the harder grasses, and separate the favorable feeding grounds as well as the drinking pools, the change of proportion is principally in the direction of *elongation* of the feet, the teeth, and the skull respectively, or dolichopody (feet), hypsodonty (teeth), and dolichocephaly (skull).

Primitive and progressive foot structure. — It is surprising how little attention was given to the feet of mammals between the time of Cuvier and that of Gaudry, Kowalevsky, Huxley, and Cope. Cuvier himself had assembled a lot of wholly unrelated animals as "Les Pachydermes" because of the common possession of a thick skin; this was virtually a new designation for the assemblage termed 'Multungula' by Storr (1780). In this unnatural assemblage consorted the thick-skinned rhinoceroses, hippopotami, and other quadrupeds. De Blainville (1816) founded the modern classification of the ungulates by observing the number of digits in the feet and separating certain of the Herbivora into two classes, "à doigts pairs" and "à doigts impairs," or with an even and an odd number of toes respectively. This suggested to Owen (1847) the separation of the Artiodactyla (ἄρτιος, even in number, δάκτυλος, finger) from the Perissodactyla (περισσός, odd in number, δάκτυλος, finger), including the sharp separation between hippopotami with their even toes and rhinoceroses with their odd number, into two distinct orders. Thus attention was concentrated upon the *numerical* changes in the evolution of the feet, and Huxley, Kowalevsky, and Cope more or less independently reasoned that hoofed animals with one, two, three, and four toes must have sprung from more primitive forms with five toes. The number of digits, therefore, became an important means of distinguishing the adaptive stages of evolution in many different lines of mammals, as follows:

Pentadactyl, primitive five-toed mammals such as *Phenacodus.*
Tetradactyl, mammals with four digits such as *Hippopotamus* and dog.
Tridactyl, mammals with three digits such as *Rhinoceros* and early stages in the evolution of the horse.
Didactyl, mammals with two digits such as the deer and cattle.
Monodactyl, mammals with one digit, typified by the horse.

It was also observed that the simple number of digits does not tell the whole story because of differences of proportion related to the amount of service which each digit renders to the animal. Thus in an early stage in the evolution of the horse there are three full-sized digits and a short additional digit in process of degeneration. The former rest on the ground and are functional or in active service; the latter is suspended at the side of the foot, has lost contact with the ground, and is becoming vestigial. This gave rise to a distinction between functional tridactylism, in which all three toes are of service, and numerical tridactylism, as in *Hipparion*, where the middle toe is doing all the work, and the two side toes are dangling above the ground. De Blainville's (1816) and Owen's (1847) separation of the even- and odd-toed hoofed animals led to the observation that the main weight of the animal either passes through the central digit, as in the rhinoceros and horse (Perissodactyla) or between the two cen-

tral digits (Artiodactyla). This difference was expressed in other words by Marsh [1] by the terms *Mesaxonia* and *Paraxonia* respectively.

The pose or angle of the foot as a whole, including the wrist and ankle joints (carpals and tarsals), the intermediate bones (metacarpals and metatarsals), and the terminal joints (phalanges and ungues), began to

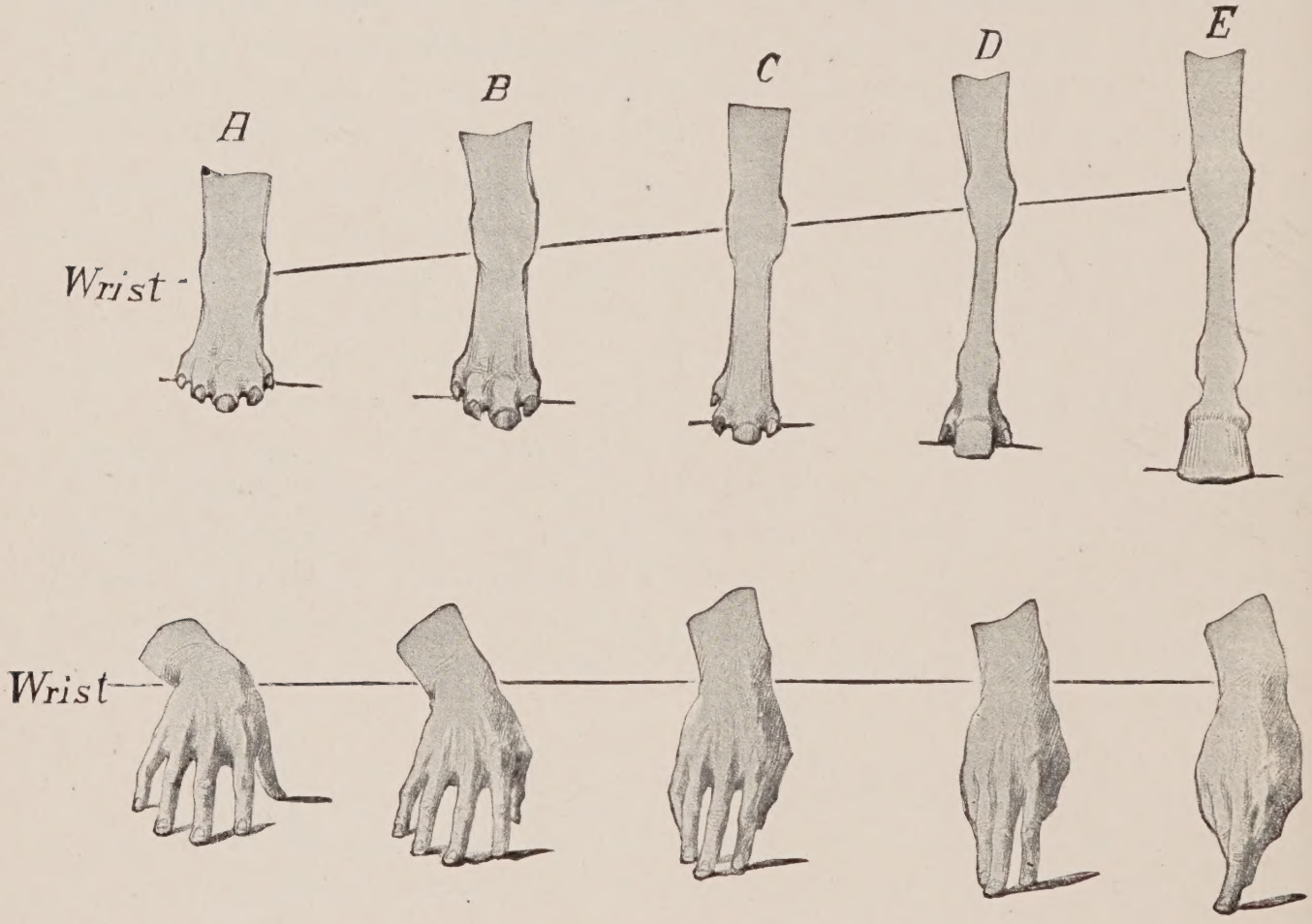


FIG. 5. — Evolution from pentadactyl to monodactyl condition as illustrated in the foot of the horse (above) ; comparison with the human hand (below). *A*. Pentadactyl, hypothetical ancestral stage. *B*. Tetradactyl, *Protorohippus* stage. *C*. Tetradactyl-tridactyl, *Epihippus* stage (three toes resting on the ground, one raised slightly above). *D*. Tridactyl, *Mesohippus* stage. *E*. Monodactyl, *Equus* stage.

attract increasing attention. In primitive forms it was seen that the entire hand and foot is stretched along the ground, as in the bear and in the foot of man, while in the opposite extreme the foot rests on the nail or on the very extremity of the last phalanx, as in the hoof of the horse. Thus in the *gradus*, or step, a series of important intermediate stages are observed, as follows:

PLANTIGRADISM, where the entire sole of the hand or foot rests upon the ground, as in the hind foot of the bear.

SEMI-PLANTIGRADISM, where half the sole rests upon the ground, as in the fore foot of the bear.

[1] Marsh, O. C., Dinocerata. A Monograph of an Extinct Order of Gigantic Mammals. *U. S. Geol. Surv.*, Vol. X, Washington, 1884, p. 186.

DIGITIGRADISM, where the foot rests only on the rows of phalanges, as in the dog and cat.

UNGULIGRADISM, where the foot rests only upon the end phalanx, as in the horse and the deer.

RECTIGRADISM, where the foot is immobile and the entire weight rests on a large pad, as in the elephant.

Reduction of digits. — This led to the further generalization that all primitive types of mammals were pentadactyl or five-fingered and plantigrade, or with the sole of the hand and foot resting upon the ground. From this it was an easy step to perceive that the raising of the wrist and ankle joints from the ground in the passage from plantigradism to digitigradism also tended to raise the shorter digits, namely, the thumb, or first digit in the hand, and the big toe, or first digit in the foot, from the ground, to render them useless in progression and to initiate their degeneration or retrogression. It is, in fact, in this stage, where the inside digits of both hand and foot are in process of disappearance, that we discover most hoofed mammals of the early geological periods. The loss of one digit after another occurs under what is known as the *law of digital reduction.* Thus the passage from five to four, to three, to two, to a single digit is a gradual process, not the work of a century or centuries, but of vast periods of time.

Perfection of joints and facets. — Another and more intricate law in the science of foot evolution concerns the changes in the articulations, or facets, between the bones of the wrist and ankle and the bones of the metapodium on which they rest.

Kowalevsky first directed close attention to the fact that all these facets and articulations are altered while the wrist or ankle is in process of becoming raised from the ground, while the digits are being reduced, and while the weight is being concentrated more and more on the central digits and taken from the lateral digits. This shifting of the joints or facets was found by Kowalevsky,[1] Cope,[2] Rütimeyer,[3] and Osborn[4] to produce an interlocking system, so that the bones are placed above each other like rows of bricks with "struck" or alternating joints, and this alternation of the joints with the closed surfaces is brought about by more rapid growth of some parts of the foot bones than of other parts, producing at every stage a perfect mechanism, calculated to resist the enormous strains which come upon the foot, especially in the rapid movements of swift running

[1] Kowalevsky, Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer natürlichen Classification der fossilen Hufthiere. *Paläontographica*, Vol. XXII, 1873.

[2] Cope, The Vertebrata of the Tertiary Formations of the West. *Rept. U. S. Geol. Surv. Terr.*, Vol. III, Washington, 1884; also, The Perissodactyla, *Amer. Natural.*, Vol. XXI, 1887.

[3] Rütimeyer, L., Über einige Beziehungen zwischen den Säugethierstämmen Alter und Neuer Welt. *Abh. Schweiz paläont. Ges.*, Vol. XV, pp. 1–151, Zürich, 1888.

[4] Osborn, The Evolution of the Ungulate Foot, Pt. IV of The Mammalia of the Uinta Formation by Scott and Osborn. *Trans. Amer. Philos. Soc.*, n.s. Vol. XVI, Aug. 20, 1889, pp. 531–569.

types of hoofed animals. Another device of nature in the same direction is the development of tongue-and-groove joints out of rounded or universal joints, bringing about precision of movement and preventing lateral dislocation. All these steps seem to have a distinct survival value, that is, to affect mammals in the struggle for existence. Thus Kowalevsky was the first to point out that certain quadrupeds with less perfected foot mechanisms were gradually replaced by others with more perfected foot mechanisms.

A lowly organized or primitive hoofed mammal is found to be full of mechanical defects when its feet are applied to the severe tests of rapid progression; it is *condylarthrous*, 'ball and socket' or loose-jointed, it is *plantigrade*, or clumsy, or slow-gaited, it is *pentadactyl*, or with five fingers

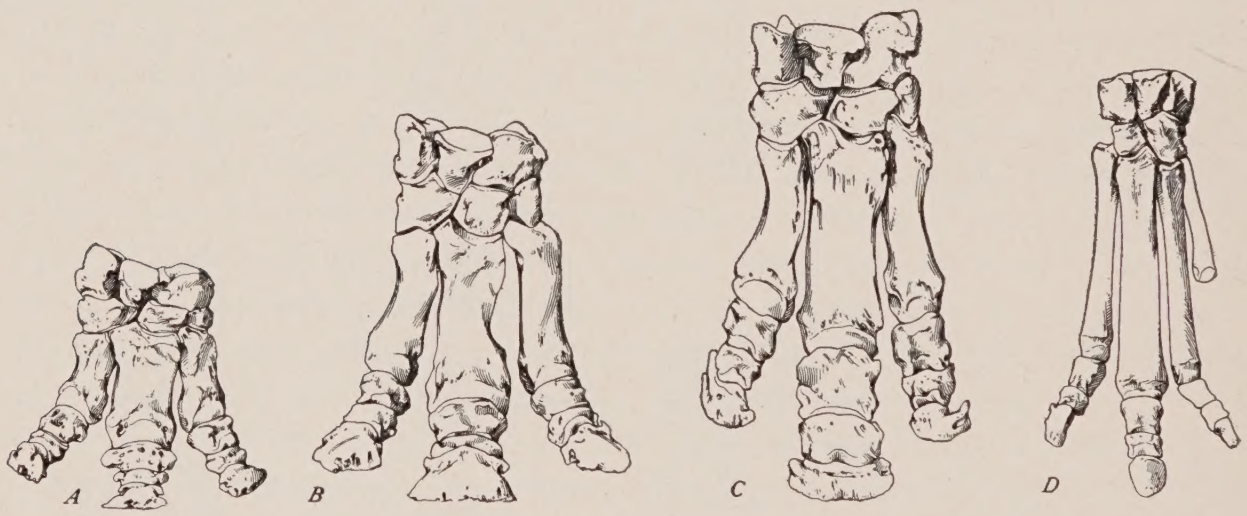


FIG. 6. — Foot proportions among rhinoceroses. *A*. Brachypody, short-footed, *Teleoceras fossiger*. *B*. Mesatipody, medium-footed, *Aphelops malacorhinus*. *C*. Mesatipody, medium-footed, *Rhinoceros unicornis*. *D*. Dolichopody, long-footed, *Colodon longipes*.

still resting on the ground, it is often *taxeopod*, or with imperfectly alternating joints in the different rows of bones in the hands and feet. As a rule also it is short-footed, or *brachypod*.

In short, all the ancestral adaptations to ambulatory, tree, and rock-climbing purposes must be abandoned and new adaptations acquired.

Like the teeth, the feet evolve partly through changes of *proportion* as well as through *reduction*, or loss of useless parts. Thus the passage from slow-walking, or ambulatory types, to swift-moving, or cursorial types, is almost invariably marked by elongation of the primitively short hand and foot. This gives us another series of stages, as follows:

MESATIPODY, mean, or intermediate foot forms, as of the tapir.
BRACHYPODY, extremely short feet, as of the elephant.
DOLICHOPODY, elongate foot forms, as of the horse.

Altogether the changes of foot structure in the hoofed animals constitute a fascinating study and are easily comprehended. Through these changes the prehensile and locomotor powers of the limbs of animals are

profoundly affected and diversified, and numbers of types are evolved, as, for example:

AMBULATORY, slow-moving, mostly primitive.
CURSORIAL, swift-moving, secondary.
SALTATORIAL, swift-moving, leaping, secondary.
FOSSORIAL, slow-moving, digging, and burrowing.
NATATORIAL, amphibious, aquatic, swimming.
ARBOREAL, slow-moving, tree-climbing.
GLISSANT, gliding, as in the 'flying' squirrel.
VOLANT, flying, as in the bat.

Primitive and progressive skull structure. — Changes in tooth proportion and foot proportion may or may not be accompanied by changes of propor-

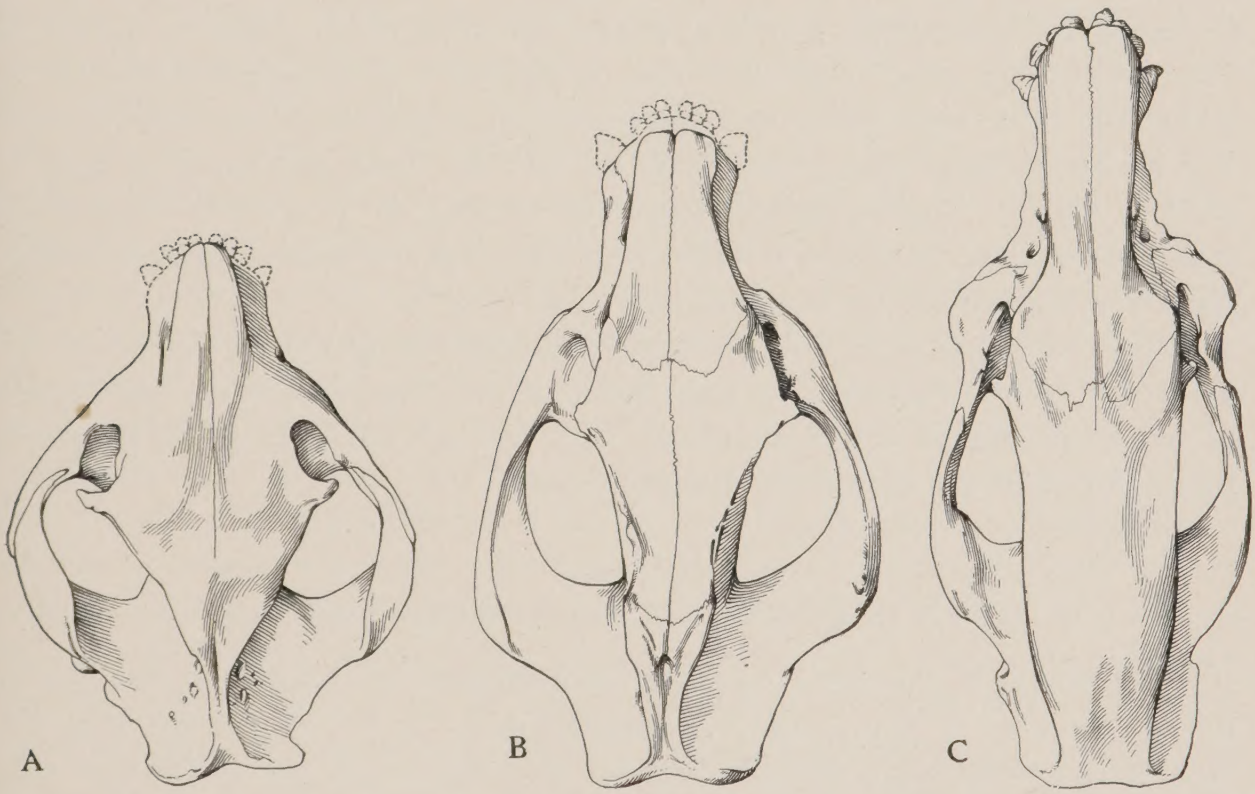


FIG. 7. — Skull proportions among Titanotheres. *A.* Brachycephaly, short-headed, *Palæosyops major*. *B.* Mesaticephaly, medium-headed, *Manteoceras manteoceras*. *C.* Dolichocephaly, long-headed, *Dolichorhinus cornutus*.

tion in the skull. Here again we find that there are three general stages in the anatomy of the skull of mammals,[1] and that the descriptive terms are the same as those which were introduced long ago (1842) in the anatomy of the human skull by the great Swedish anthropologist, Anders Adolf Retzius (1796–1860), namely:

MESATICEPHALY, an intermediate or partly elongated condition, characteristic of many intermediate and primitive forms, such as the tapir.

[1] See Osborn, H. F., Dolichocephaly and Brachycephaly in the Lower Mammals. *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI, Art. VII, Feb. 3, 1902, pp. 77–89.

Brachycephaly, a short, broad-headed condition of the skull, characteristic of some progressive forms.

Dolichocephaly, an elongate condition of the skull, especially of the anterior or facial portion in front of the eyes, as in the horse (*Equus*) and in the moose (*Alces*).

The rationale of these changes of proportion is very different in different skulls, so that we never can assume that long-headedness is due to any single cause. In the horse long-headedness is a very ancient character; even the earliest known four-toed horses have quite elongate, or at least mesaticephalic, skulls. The progressive elongation of the skull in horses is apparently for two purposes: first, to facilitate reaching the ground with the row of incisor or cropping teeth; second, and no less important, to allow space in front of the eye sockets for the great rows of elongate, or hypsodont, grinding teeth, the marvelous dental battery of the horse. We might assume from these facts that long-headedness is correlated with long teeth, but the giant pigs (elotheres) have still longer and narrower skulls than the horse, yet all the teeth are brachyodont, or short-crowned. Again, the elephant has extremely elongate or hypsodont molar teeth, yet it possesses also the shortest, or most brachycephalic, skull known among the Mammalia.

Thus all kinds of combinations and changes of proportion occur in the evolution of mammals. The correlation is not that of certain fixed types of structure, but it is a correlation of perfect adaptations to different demands brought about by the changes in habitat.

II. Mammals and their Environment

The fitness of mammals to their environment takes us back to another line of thought in the history of palæontology, in which we see that the idea of the *evolution of the environment*, as revealed by the study of fossils and the earth itself, grew step by step with the idea of the evolution of mammalian life. It has become clear that there are two ways in which mammals experience a change of environment: either through their own migrations, or through "the migration of the environment itself," as Van den Broeck has expressed it, in the successive historic changes of certain parts of the earth in course of time. Thus if we imagine a family of mammals residing continuously in the region now known as South Dakota, the early humid environment has migrated to quite a different part of the American continent, and an entirely new, arid environment has come in. Sometimes mammals and their environment migrate together. This was certainly the case during the Glacial Period, when physiographic conditions, faunas, and floras all moved southward together before the advance of the ice sheet, and again moved northward together as the ice retreated.

Origin and Migration

The crude idea of *centers of origin* and dispersal, or migration of different kinds of animals, is a very ancient one. Even Moses' treatise on Noah's ark and the spread of its passengers was probably not the first attempt at a theory of geographic origin and distribution of the beasts and birds, because this theory had its antecedents in the traditions of Mesopotamia. There is no question that these myths strongly influenced the early attempts at scientific explanation. For the approaches to modern views one should read successively the writings of the great French naturalists Buffon and Cuvier. We find in Buffon,[1] who wrote in the middle of the eighteenth century, many instances of anticipation of what are commonly regarded as modern views.

Buffon's laws of animal distribution were regarded by Cuvier as veritable discoveries. They set forth some of the fundamental principles of geographic distribution, contrasting successively all the continents (Europe and Asia, or *Eurasia*, Africa, North America, and Australia), and enumerating especially the kinds of animals which each possessed and in which each was lacking. In comparing the new and old worlds, Buffon observed that the quadrupeds of North America were of smaller size than those of Eurasia and Africa, since the largest North American animals were inferior to the elephants, rhinoceroses, and hippopotami of Africa. His second remark is more important: it is, that the North American animals form a parallel or collateral animal kingdom which more or less duplicates that of the Old World with some important exceptions, and this remark may be construed as an anticipation of the *law of evolution of analogous groups* on large continental surfaces. Every animal, he remarked further, has its natural country or habitat, a fact which links zoölogy with geography. His theory of evolution — and he certainly was an evolutionist — may be known to-day as *Buffon's law* of the direct action of the environment upon the organism; he believed that climate or environment exerted the strongest influence in the modification of animal forms. Thus he attributed the shades of color in the skin of human races to the more or less intense action of the sun.

Palæogeography, or the study of the past relations of the land and sea surfaces of the globe, also had its beginnings in Buffon's time. In commenting on the giant extinct fauna, the mammoths (*Elephas primigenius*) and woolly rhinoceroses (*Rhinoceros tichorhinus*), which had been made known in northern Asia and Siberia through the explorations of Pallas, and on the former distribution of the elephants in North America, Buffon significantly pointed out that parts of the globe now submerged beneath

[1] Georges Louis Leclerc, Comte de Buffon, 1707–1788. Edition of Buffon's works here referred to is the first, Histoire naturelle générale et particulière, avec la description du cabinet du Roi, 1749–1789, 44 vols., illustrated, including Supplements. Flourens's Buffon, Histoire de Ses Travaux et de Ses Idées, 12mo, Paris, 1844, is based on this edition.

the sea were formerly elevated and furnished land bridges or connections between the continents; he thus clearly adumbrated the idea of the migrations of quadrupeds and of the subsequent separation of faunas, or animal groups, by continental depressions and the submergence of old migration routes.

The accompanying map, the dotted areas on which represent the land bridges which would emerge through the elevation of the continental borders to a height of two hundred fathoms, shows the reader that no

FIG. 8. — Map of the world with existing outlines and 200 fathom lines (dotted areas) showing former land connections at the last period of maximum elevation.

very profound or cataclysmal changes are required to connect the northern continents with each other and with the outlying masses. With the southern continents, South America, Africa, and Australia, it is different; an emergence of 3040 meters, or 1662 fathoms, is necessary to connect them as shown on the map on p. 77.

Still more definitely Buffon placed the land separation between the old and new worlds in his "Sixth Epoch," and in this connection clearly brought out a *theory of extinction* of certain species, as of the mammoths of Siberia and of North America. This problem of the interpretation of the giant fossils of the north had been one of the first to attract the attention of naturalists; Johann Georg Gmelin (1709–1755) left it as a legacy to Buffon, Buffon handed it down to Blumenbach, the pioneer of vertebrate palæontology in Germany. Buffon attributed (Tome V, p. 172) the disappearance of the great animals from the north partly to the refrigeration of the temperature, and partly to migration to the south. *Nous ne pouvons*

douter qu'après avoir occupé les parties septentrionales de la Russie et de la Sibérie . . . où l'on a trouvé leurs dépouilles en grande quantité, ils n'aient ensuite gagné les terres moins septentrionales . . . en sorte qu'à mesure que les terres du Nord se refroidissoient, ces animaux cherchoient des terres plus chaudes. . . . (Tome V, p. 172, Supplément.) This sagacious naturalist also pointed out that these monuments of the extinct life of the earlier ages of the world were understandable by comparison of their structure with that of living animals of related type; such comparison, he observed, demonstrates the existence in times past of species different from those actually existing but closely related (Tome V, p. 154, Minéraux).

Cuvier observes that fossils, which have given birth to the theory of the earth, have also furnished it with its principal lights, the only ones which have been generally recognized down to the present period. He extends Buffon's ideas, and gives new and beautiful theoretical illustrations of the possible effects of continental elevation and depression, which we may paraphrase with slight modifications of his own language.

Let us suppose, Cuvier remarks in his *Discours* (Paris, 1826, pp. 64–65), that a great invasion of the sea covers with a mass of sand or other deposit the continent of Australia; it would bury the carcasses of the kangaroos, wombats, dasyures, bandicoots, flying phalangers, as well as of the duck-bills [*Ornithorhynchus*] and spiny anteaters [*Echidna*]. It would entirely destroy these species of animals because none of them exist in any other country. Suppose, further, that the same convulsion of nature were to leave dry the numerous small straits which separate Australia from the continent of Asia; it would open the way for the entrance into Australia of the elephant, rhinoceros, buffalo, horse, camel, tiger, and all other Asiatic quadrupeds, which would come to people this continent in which they were before unknown. If, however, a naturalist studying these living animals were to lay open the soil on which they moved he would find the remains of the buried ancient fauna of marsupials, etc. What Australia would become were such a hypothetical invasion realized, Europe, Siberia, and a great portion of America are to-day, and it may some day be discovered in the examination of these countries, and even of Australia itself, that they have all experienced similar revolutions. To carry the above hypothesis still further, Cuvier concludes, after the Asiatic animals have migrated into Australia let us imagine that a second revolution destroyed Asia, the original home of these animals: the naturalist who discovered their second country would be as much embarrassed to find whence they came as we can now be to discover the origin of those animals which are found in our own countries.

Despite these sagacious views, Cuvier was an exponent of the cataclysmal rather than the uniformitarian school of transformation, that is, he believed in violent changes in past times rather than in the slow changes such as we observe to-day. Experience has proved that he was somewhat

extreme in his idea of the *total* depopulation of the continents through great physical revolutions; we have no evidence that such sweeping changes have ever occurred, yet he was not far from the truth, and it is certain that in these specific illustrations, cited above, he clearly thought out and furnished some of the chief ideas underlying our modern work, namely, of the invasions of great groups of mammals through the formation of new routes for migration and of wide resulting contrasts between the existing and the extinct forms of life, or faunas in all continental areas.

As regards mammalian origin and descent it is well known that Cuvier was not an evolutionist, but on the contrary a convinced believer in special creation. This belief kept him from fully anticipating the ground work of modern palæontology. He did not consider the Age of Mammals as furnishing the source of any animals now existing. He recorded his discovery of the mammals of the *Gypse de Montmartre* as a revelation of a phase of mammal life which he believed to belong early in the Age of Mammals (it is now known to be Upper Eocene), but he did not seek among these mammals ancestors of existing forms. Although he believed that all these older forms had become extinct, he did not appeal to *new creations* to produce the species now existing, but maintained that such species were existing elsewhere, that is, in other parts of the world. This ingenious and interesting feature of Cuvier's theories as to the *replacement of faunas* has not been understood sufficiently because, as recently pointed out by Depéret,[1] he has been credited generally with a theory which really arose in the imagination of some of his followers rather than his own, namely, of a succession of extinctions followed by a *succession of creations*. Cuvier rather believed that an extinction on one continent or in one region was followed by repopulation through migration from another region, and he illustrated his meaning very clearly in the hypothetical cases cited above of the possible invasion of the sea over the continent of Australia and subsequent repopulation from Asia.

The Law of Adaptive Radiation

The law of evolution even as crudely perceived by Buffon added another element of fascination to the ideas of centers of origin and of migration, namely, that of modification of mammals under new and strange conditions of environment. Such general modification was about as far as Buffon's thoughts went. Those of Lamarck went farther, namely, to adaptation to new conditions of life, and with this idea is coupled his conception of the *principle of divergence or radiation* in the formation of different habits and the search for different kinds of food.

[1] Depéret, L'évolution des Mammifères tertiaires; l'importance des migrations (Eocène). *C. R. Acad. Sci.*, Paris, Vol. CXLI, Nov. 6, 1905, p. 702.

Darwin independently and at a somewhat late day discovered this essential principle as told in his Autobiography:[1]

"But at that time I overlooked one problem of great importance; and it is astonishing to me, except on the principle of Columbus and his egg, how I could have overlooked it and its solution. This problem is the tendency in organic beings descended from the same stock to diverge in character as they become modified. That they have diverged greatly is obvious from the manner in which species of all kinds can be classed under genera, genera under families, families under suborders and so forth; and I can remember the very spot in the road, whilst in my carriage, when to my joy the solution occurred to me; and this was long after I had come to Down. The solution, as I believe, is that the modified offspring of all dominant and increasing forms tend to become adapted to many and highly diversified places in the economy of nature."

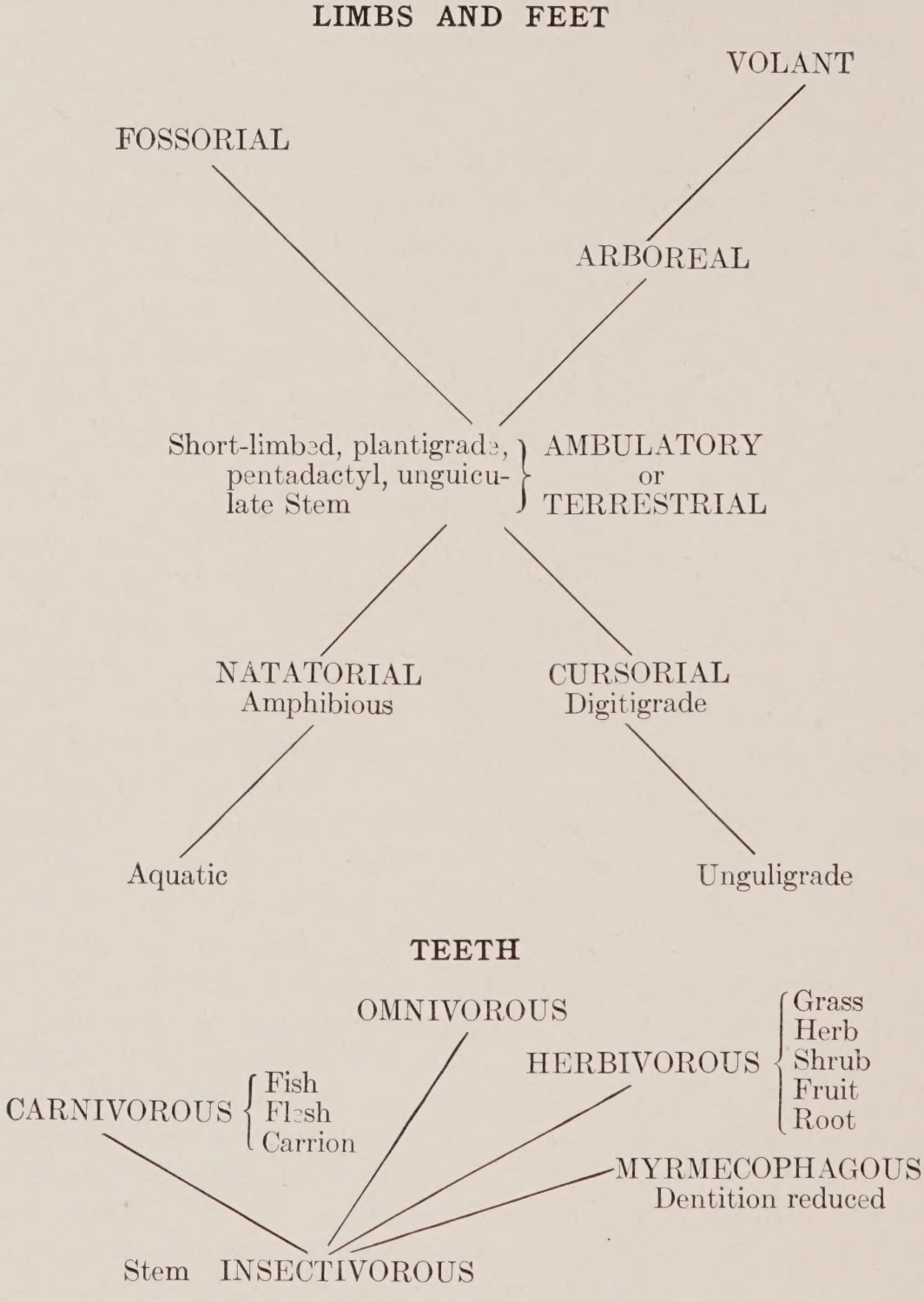
The writer has termed this principle of *embranchement* of Lamarck, or of divergence of Darwin, the *law of adaptive radiation*.[2] According to this law each isolated region, if large and sufficiently varied in its topography, soil climate, and vegetation, will give rise to a diversified mammalian fauna. From primitive central types branches will spring off in all directions with teeth and prehensile organs modified to take advantage of every possible opportunity of securing food and in adaptation of the body, limbs, and feet to habitats of every kind, as shown in the diagrams on page 24. The larger the region and the more diverse the conditions, the greater the variety of mammals which will result.

The most primitive kinds of mammals were probably small insectivorous or omnivorous forms, therefore with simple, short-crowned teeth, of slow-moving, ambulatory, terrestrial, or arboreal habit, and with short feet provided with claws.

In seeking food and avoiding enemies in different habitats the limbs and feet radiate in four diverse directions; they either become *fossorial* or adapted to digging habits, *natatorial* or adapted to *amphibious* and finally to *aquatic* habits, *cursorial* or adapted to swift-moving, terrestrial progression, *arboreal* or adapted to tree life. Tree life leads as its final stage into the parachute types of the flying squirrels and phalangers, or into the true flying types of the bats. We have not thus far found a single instance in which a mammal is known to have been transformed from an aquatic into a land type; it is always the reverse. Nor have we found an instance where the extreme fossorial or cursorial types have retrogressed into slow-moving, ambulatory, or terrestrial types. There is some evidence, however, of arboreal types secondarily taking up terrestrial habits, as in the case of many of the terrestrial and cursorial marsupial mammals of Australia, which are believed to have evolved from specialized arboreal

[1] The Life and Letters of Charles Darwin, including an Autobiographical Chapter. Edited by his son Francis Darwin. London, 1888, Vol. I, pp. 68–69.

[2] Osborn, The Law of Adaptive Radiation. *Amer. Natural.*, Vol. XXXIV, 1902, pp. 353–363.



forms. Similarly, Matthew [1] has suggested that most placental mammals bear evidence of descent from primitive arboreal ancestors.

Similarly, in the case of the teeth, insectivorous and omnivorous types appear to be more central and ancient than either the exclusively carnivorous or herbivorous types. Thus the extremes of carnivorous adaptation, as in the case of the cats, of omnivorous adaptation, as in the case of the bears, of herbivorous adaptation, as in the case of the horses, or myrmecophagous adaptation, as in the case of the anteaters, are all secondary.

[1] Matthew, W. D., The Arboreal Ancestry of the Mammalia. *Amer. Natural.*, Vol. XXXVIII, nos. 445–446, Nov.–Dec., 1904.

It is obvious that a mammal may hunt for its herbivorous diet in several different habitats, in the water, on land, on trees, beneath the surface of the earth, and since the limbs are the means of locomotion in these habitats a mammal may be herbivorous and natatorial, like the manatee (*Manatus*) and dugong (*Halicore*), herbivorous and arboreal, like the tree sloths (Bradypodidæ), herbivorous and cursorial, like the horses. This makes it perfectly clear why there is no fixed correlation between the structure of the teeth and that of the limbs, and is another proof of our inability to predict the form of one part of an animal from our knowledge of another part.

The prolonged operation of the adaptive radiation of mammals from primitive and generalized forms into specialized and adaptive forms has in the vast periods of geologic time (see p. 63) evolved or created the existing *Orders of Mammals.*

The Orders of Mammals[1]

A brief review of the chief kinds of mammals living and extinct is needed before we can take a survey of their history; otherwise the reader will be lost in details without being able to comprehend general kinds and relations. A full conspectus of the classification of the principal types of mammals living and extinct will be found in the Appendix of this volume, to which the student or reader may make rapid reference through the index.

With reference to adaptive radiation, each order of mammals should be thought of as having a *typical mode of life* from which its various members diverge in various degrees, sometimes so far as to take up an entirely different mode of life. The typical life is usually the original, ancestral or primitive life which characterized the order when it first diverged from other orders; as a rule it is the typical mode of life which gives or has given the dominant or profound anatomical characters to the teeth and skeleton. For example, the rodents were originally herbivorous, gnawing animals, and this is still typical of most rodents, but certain rodents have departed so far from their ancestral habits as to become not only aquatic but fish-eating. Thus there is a clear distinction between the primary, typical, original, fundamental adaptation of an order, and the *secondary* or acquired adaptations which many of its members may enter upon and thus imitate the typical adaptation of another order.

The grand divisions and subdivisions of the Class Mammalia of Linnæus are as follows:

[1] For a review of the evolutionary relationships of the principal groups of mammals, see Gregory, W. K., The Orders of Mammals. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVII, 1909.

A. EGG-LAYING MAMMALS. Very Primitive, Reptile-like, or Transitional, Reproducing their Young from Deposited Eggs.

I. **PROTOTHERIA.**

1. PROTODONTA. Very small and primitive, North American mammals (?) of the early Age of Reptiles.

2. MONOTREMATA. Of Australia, New Guinea, and Tasmania, highly specialized Prototheria. No Pre-Pleistocene forms certainly known. Duckbill Platypus (*Ornithorhynchus*) and Spiny Anteater (*Echidna*).

B. VIVIPAROUS MAMMALS. Of Higher Grade, Bringing Forth their Young Alive.

II. **MARSUPIALIA, DIDELPHIA,** or **METATHERIA.** Pouched Mammals, or Marsupials, typically carrying the young in a pouch. Placental structure rudimentary or primitive. Extinct and living families of Australia, South America, and (opossums, etc.) Holarctica.

1. TRICONODONTA. Polyprotodont carnivorous marsupials (?) of the Age of Reptiles.

2. MARSUPIALIA PROPER.

a. *Multituberculata.* Diprotodont, herbivorous marsupials of the Age of Reptiles and early Age of Mammals.

b. *Polyprotodontia.* Polyprotodont, carnivorous, and omnivorous Marsupials of the Age of Mammals. Opossums, dasyures, etc.

c. *Diprotodontia.* Diprotodont, herbivorous marsupials of the Age of Mammals. Phalangers, kangaroos, etc.

III. **PLACENTALIA, MONODELPHIA,** or **EUTHERIA.** Mammals nourished before birth by a typical placenta. Young never carried in a pouch.

A. *UNGUICULATA.* Clawed Mammals, adapted to terrestrial, fossorial, arboreal, aquatic, cursorial, and volant life. Including all the actual and theoretical primitive forms of mammals, as well as many modernized or highly specialized forms.

1. PANTOTHERIA (TRITUBERCULATA). Small primitive insectivores of the Age of Reptiles (Jurassic), generally with numerous cheek teeth.

2. INSECTIVORA. Modern insectivores, such as moles, shrews, hedgehogs, and tenrecs.

3. TILLODONTIA. Lower to Middle Eocene, tillotheres or tillodonts, herbivorous or phytophagous mammals, in some respects similar to rodents.

4. DERMOPTERA. Represented only by the "flying lemur," *Galeopithecus*, of the Oriental region.

5. CHIROPTERA. The bats, including the fruit bats, vampires, insect-eating bats, etc.

6. CARNIVORA.

   a. *Creodonta*, or Primitive Carnivora (Eocene). Surviving to the Lower Oligocene.

   b. *Fissipedia*, of Middle Eocene to recent times, including the civets, hyænas, dogs, raccoons, bears.

   c. *Pinnipedia*. Seals, walruses. Known from Miocene to recent times.

7. RODENTIA. Squirrels, beavers, mice, porcupines, etc. Lower Eocene to recent times.

8. TÆNIODONTA, or GANODONTA. Probably ancestral or related to the edentates. Primitive, with enamel on the teeth. Basal to Middle Eocene, North America only.

9. EDENTATA, or XENARTHRA. True South American edentates (also North America, Eocene and Recent), without enamel on the teeth, Eocene to Recent. Sloths, armadillos, glyptodonts, ground sloths, ant-bears, etc.

10. PHOLIDOTA. Scaly Anteaters, or Pangolins (*Manis*), of India and Africa. Oligocene to recent times.

11. TUBULIDENTATA. Aardvarks (*Orycteropus*). Oligocene to recent times. Africa (recent species), and Europe (extinct species only).

B. *PRIMATES*, primarily adapted to arboreal and ambulatory life, fingers terminating in "nails," rarely in claws. Frugivorous, phytophagous, and omnivorous. The primitive forms are distantly allied to the Unguiculata-Insectivora.

12. PRIMATES, including

   a. *Lemuroidea*, lemurs, galagos, "aye-aye," tarsier, etc., and extinct lemuroids. Eocene to recent times.

   b. *Anthropoidea*, monkeys and apes, including South American marmosets, Old World monkeys, baboons, apes, and anthropoid apes, also man. Miocene to recent times.

C. *UNGULATA*, or HOOFED MAMMALS, herbivorous, primarily ambulatory and cursorial, secondarily aquatic and rarely arboreal. Originally derived from members of the Unguiculata.

1. ARCTOGÆAN HOOFED MAMMALS

i.e. of North America, Asia, Europe, and Africa.

A. Probably of Holarctic Origin.

13. CONDYLARTHRA. Archaic, primitive, light-limbed, hoofed mammals, surviving to the Lower Eocene.

14. AMBLYPODA. Archaic, heavy-limbed quadrupeds, surviving to the Upper Eocene.

15. ARTIODACTYLA. Even-toed, hoofed mammals, including pigs, hippopotami, camels, tragulines, deer, giraffes, antelopes, sheep, oxen, and many extinct forms. Lower Eocene to recent times.

16. **Perissodactyla.** Odd-toed, hoofed mammals, Lower Eocene to recent times, including tapirs, horses, rhinoceroses, and the extinct palæotheres, titanotheres, lophiodonts, etc.

17. **Ancylopoda.** Closely related to the Perissodactyla. Middle Eocene to Upper Miocene times, with hoofs secondarily modified into claws, partly for digging.

B. Probably of African Origin.

18. **Proboscidea.** Mastodons and elephants. Upper Eocene to recent times.

19. **Barytheria.** Including only one (discovered) large, peculiar herbivore, of the Lower Oligocene of North Africa.

20. **Sirenia.** Sea-cows or manatees, and dugongs. A highly modified aquatic offshoot of the hoofed mammals. Upper Eocene to recent times.

21. **Hyracoidea.** The dassies and conies of Africa and Syria, small rock and tree-living hoofed animals. Upper Eocene to recent times.

22. **Embrithopoda.** Including the "Arsinoïtheres" of the Upper Eocene and Oligocene of northern Africa only.

2. NEOGÆAN HOOFED MAMMALS OR NOTOÜNGULATA
i.e. of South America.

23. **Homalodotheria.** Including *Homalodotherium* and others. Pentadactyl, secondarily clawed mammals. Teeth in continuous series. Eocene to Miocene, South America.

24. **Toxodontia.** Including the protypotheres, typotheres, nesodonts, and toxodonts. Eocene to Pleistocene, South America. Molars with flattened outer wall, more or less rhinocerotoid. Incisors often enlarged.

25. **Astrapotheria.** Including the rhinoceros-like astrapotheres. Chiefly Miocene, South America. Upper canines forming elongate tusks. Limbs pillar-like.

26. **Litopterna.** Including light-limbed, three-toed, and virtually one-toed forms, some resembling three-toed horses. Eocene to Pleistocene, South America.

27. **Pyrotheria.** Including 'diprotodont' forms with crested mastodon-like molar teeth. Eocene, South America. Limbs pillar-like.

D. CETACEA, or whales, aquatic mammals probably derived from the Unguiculate Division.

28. **Zeuglodontia.** Primitive Eocene whales, transitional in certain characters to primitive carnivores.

29. **Odontoceti.** Toothed whales, including the extinct squalodonts, the river and marine dolphins, the belugas and narwhals, the beaked whales, and the sperm whales.

30. **Mystacoceti.** Whalebone whales, including the right whales, the humpbacked whales, and the fin-backed whales.

This classification is followed in the same order in the Appendix of this volume, where the families and principal genera are also introduced.

Adaptive Radiation and Geography

We may now consider the relation between the adaptive radiation of the different kinds of mammals and the geography of past and present times.

Adaptive radiation, continental.[1] — The law of adaptive radiation naturally operates on a grand scale on great continents like Africa, or a great insular continent like Australia. Through its geographic distribution and isolation there originate from common primitive forms new species, genera, families, and even orders of mammals. It is most important to grasp in imagination the ideas of adaptive radiation as applying wherever there is a large theater for the operation of this law and of a succession of radiations in the course of the Age of Mammals. Thus we shall study the proofs of primeval or archaic radiation of mammals which began during the Age of Reptiles and extended in all directions into forms resembling modern insectivores, rodents, bears, dogs, cats, monkeys, sloths, bunodont, and selenodont hoofed mammals and lophodont hoofed mammals. Through the extinction of many of these mammalian branches or radii, through the survival of other branches, or through the invasion or entrance of branches from some distant radiation, the process begins over again.

For these grand continental radiations there seems to be some ratio between the degree or extent of divergence and the physiographic diversity and extent of the geographic area in which the radiation occurs. As shown below (p. 38) this connects adaptive radiation with the science of zoögeography or geographic distribution.

Thus the highly diversified land area of Arctogæa, comprising Africa, Eurasia, and North America, constituted a vast center in which twenty-one primitive and specialized orders of mammals radiated from each other. In the more restricted continent of South America four to five orders of mammals enjoyed their chief radiation.

Adaptive radiation, local.[2] — Quite as important although not on so grand a scale is the local adaptive radiation in the same or neighboring geographic regions wherever there is found a diversity of habitat and of food supply. Good living illustrations of this *local adaptive radiation* are seen in the geographic distribution in Africa, previous to the extinction by man, of the "white" or square-lipped rhinoceros (*Rhinoceros simus*), which lives upon grasses and has long-crowned or hypsodont teeth, and the "black" or

[1] See Osborn, Correlation between Tertiary Mammal Horizons of Europe and North America: An Introduction to the More Exact Investigation of Tertiary Zoögeography. *Ann. N.Y. Acad. Sci.*, Vol. XIII, no. 1, July 21, 1900, pp. 49 ff.

[2] Osborn, 1902, *op. cit.*

pointed-lipped rhinoceros (*R. bicornis*), with short-crowned or brachyodont teeth, which browses mainly upon shrubs. The feeding ranges of these animals are not very far apart. They do not subsist upon exactly the same food, thus they do not compete. The grazing "white rhinoceros" is long-headed, or dolichocephalic, the browsing "black rhinoceros" is relatively short-headed, or mesaticephalic. The local adaptive radiation of the antelopes of Africa furnishes still more remarkable illustrations of the same kind.

Among living forms we find long-headed and short-headed, long-footed and short-footed, long-toothed and short-toothed types, living near each other, resorting to the same water courses for drink, and thus liable to be killed in the same spot. We thus find a clue in the present to the interpretation of what frequently occurs among fossilized types, namely: in the same geological deposits are often mingled short-footed, or ambulatory, with long-footed, or cursorial, quadrupeds. The cursorial types subsisted upon grasses and ranged out on the plains, the ambulatory types, chiefly browsers, frequented the river borders, the thickets, and the hillsides. Among the best illustrations of this kind is the difference between the forest-living horse *Hypohippus* and the plains-living horse *Hipparion* of the Upper Miocene. (See pp. 243, 295.)

Thus local adaptive radiation causes the splitting up of mammals dwelling in the same geographic regions into side branches or series which we call *phyla*. We may find preserved in the same geologic deposits two, three, four, or even as many as five phyla of mammals belonging to direct and collateral lines. Local adaptive radiation is, therefore, one explanation of the next very general principle of divergence, which may be known as the *polyphyletic law*.

The polyphyletic law. — In these locally separated phyla, sometimes minute, sometimes conspicuous differences are developed. One of the most frequent distinctions is in adaptations to speed, *i.e.*, in ambulatory and cursorial types; another is in the proportions of the skull, whether brachycephalic or dolichocephalic; a third is in the proportions of the horns, if such are developed. This law is so general in Oligocene and Miocene times that if we discover light-limbed types we may anticipate the discovery of their more slow-moving counterparts. Horses, camels, rhinoceroses, the related titanotheres, have one after another proved to break up under this polyphyletic law into grazing and browsing types, slender and heavy types, in the same or neighboring geographic regions.

It is seen at once that this *polyphyly* renders the study of *phylogeny*, or the tracing of successive lines of descent among the mammals, far more interesting and at the same time far more difficult, because the fossil remains of members of these different series or phyla are often intermingled and it is difficult to separate them. In other cases the nature of the geologic deposition affords a ready key to the separation of these phyla. For

example, sediments which we find deposited in rivers are found to contain chiefly the forest-living and slow-moving, browsing types, while deposits which were made on flood plains contain the grazing, swift-moving types. Another fact of great interest is that this separation of the quadrupeds or Herbivora naturally brought about a separation of their carnivorous enemies into powerful, short-limbed types with massive jaws, and swifter, light-limbed types, with more slender parts.

Adaptation to alternations of habitat. — In the long vicissitudes of time and processions of continental changes, animals have been subjected to alternations of habitat either through their own migrations or through the migrations of the environment itself; that is, a habitat to which an animal has become adapted may be abandoned for a long period of time and adaptations are acquired for a second habitat. Following this again, life in the first habitat may be resumed. Dr. Louis Dollo has contributed most brilliant discussions [1] to this alternation of habitat theory as applied to the interpretation of the anatomy of the marsupial mammals of Australia and of several of the orders of reptiles and fishes. Although often obscure, the anatomical proofs of adaptations corresponding to alternations of habitat are recorded both in the skeleton and in the soft parts of animals.

In his brilliant essay of 1880 Huxley [2] suggested that the primitive forms of marsupials were all arboreal, or tree-living, an hypothesis which has been abundantly confirmed by the careful studies of Dollo[1] and Bensley,[3] according to which we may imagine that the marsupials passed through: (1) a very primitive land-living, or terrestrial phase, in which the limbs would be normally developed; (2) an arboreal, or tree-living phase, in which some modifications of the limbs for grasping of the boughs would be acquired, as illustrated in the tree phalangers of Australia; (3) a secondary land-living, or terrestrial phase, in which the arboreal adaptation of the limbs is checked and a new adaptation to swift-moving, or cursorial habits is acquired, as in the kangaroos, in which the hind limbs especially are modified for leaping and rapid progression; (4) a return to arboreal life, with further adaptations for tree-living habits in limbs which have already been extremely modified in course of the earlier phases, as in the tree-kangaroos.

Improbable as such a theory of alternation of habitats appears at first to be, it is none the less supported by the strongest anatomical evidence in the study of the feet of the marsupials, in which the record of one adap-

[1] Dollo, Louis, Les ancêtres des Marsupiaux étaient-ils arboricoles? *Trav. Stat. zoöl. Wimereux*, Tome VII, 1899, pp. 188–600, pl. XII.

[2] Huxley, T. H., On the Application of the Laws of Evolution to the Arrangement of the Vertebrata and more Particularly of the Mammalia. *Proc. Zoöl. Soc.*, 1880, pp. 649–662; *Sci. Mem.*, Vol. IV, pp. 457–472.

[3] Bensley, B. Arthur, On the Evolution of the Australian Marsupialia; with remarks on the Relationships of the Marsupials in General. *Trans. Linn. Soc.*, London (2) Vol. IX, Pt. 3, 1903, pp. 83–214.

tation on another is plainly written. Similar, but less extreme examples are known among the higher placental mammals of the northern hemisphere, in which the theoretical life phases are as follows:

1. A primitive ambulatory phase of a small, slow-moving animal, of insectivorous or omnivorous type, provided with claws.

2. The transformation into an herbivorous, ambulatory type provided with more or less well-formed hoofs, adapted to terrestrial gait and relatively swift movements.

3. Partial adaptation of a slower gait, accompanied by the conversion of the hoofs into clumsy claws, adapted to digging or tearing down the smaller branches of trees, as in the larger sloths. This return of an ungulate or hoofed type back to an imitation clawed type, like that of the large ground-living sloths, occurs several times independently among the typically hoofed mammals, the most extreme case being that of the chalicotheres (*Macrotherium*), which were mistaken for giant sloths by Cuvier, but which really show a regression to an older habit. (See Fig. 130.)

The Law of Analogous Evolution

All the modes of change described above are *divergent*, or tending to separate animals from each other. If the surface of the earth were infinitely varied, and if animals had an infinite variety of means of adaptation to certain conditions, undoubtedly all families and genera of mammals would be entirely dissimilar from each other, but in comparing the habitats of mammals in different parts of the earth, among the diversities of condition we find similarities or repetitions of similar environments: each continent has its mountains, its hillsides, its plains, its pampas, river borders, swamps, deserts, grazing grounds, forests, its open country. Again, the modes of adaptation of the epidermis, of the teeth, feet, and limbs of mammals are also limited. The ingenuity of Nature in adapting animals to similar conditions is not infinite; the same devices are repeatedly employed by her to accomplish the same adaptive ends.

This repetition or duplication of habitat in different parts of the earth underlies the *law of analogous evolution*, because mammals in their adaptations to similar conditions of habitat or environment in different parts of the earth have repeatedly *converged* or come together in their external and more or less in their internal form, as well as in separate structures. As regards the similar molding of single organs in many independent groups of mammals, one of the first to trace this law in detail was W. B. Scott in his masterly paper of 1891.[1] This process of the analogous fashioning of animals which may be only remotely related or not at all related to each other is known as *homoplasy*, *parallelism*, and *convergence*. Thus

[1] Scott, W. B., On the Mode of Evolution in the Mammalia and on some of the Factors in the Evolution of the Mammalia. *Jour. Morphol.*, Vol. V, 1891, no. 3, pp. 361–378, 378–402.

homoplasy affects not only separate organs but entire types of animals, groups of families and entire groups of orders, in a manner often extremely confusing to the seeker of real ancestral relationships. Analogy, or likeness of function, through its power to transform unlike and unrelated mammals or unlike and unrelated parts of mammals into likeness, has performed such miracles that the inference of kinship or descent is often irresistible; yet it is now well understood that a deeper ancestral resemblance may closely relate animals which are externally dissimilar, while it may just as widely separate animals which are externally similar. Similar desert or steppe environments have fashioned the African jumping hare (*Pedetes*) of the Cape, the true jerboas (*Dipus, Alactaga*) of the steppes of Asia, and the American jumping mice (*Zapus*) into similar saltatorial forms, yet these are partly independent transformations. These jumping mice (Dipodidæ) are paralleled by many forms: among other rodents by the Heteromyidæ (pocket mice), among the insectivores by the elephant shrews (macroscelids), among marsupials by the rat-kangaroos (*Bettongia*), etc.

Thus analogous adaptation is the counterforce to divergence, and strongly tends to bring mammals together. Nevertheless two very important exceptions are to be noted. First, we rarely find exactly and precisely the same means adopted in several groups of organs twice over; and second, all the externally similar forms may be found on close examination to bear record of real internal and ancestral differences. Thus the marsupial mole *Notoryctes* closely parallels the placental mole *Talpa* in external appearance, but in its internal structure and dentition, in its mode of reproduction, and in its skeleton it is fundamentally different. Thus similarity of adaptation can never be mistaken by the close and logical student of anatomy for similarity of descent or of ancestry. Of these two kinds of adaptation and genetic resemblance, analogy is the woof, composed of the horizontal strands which tie animals together by their superficial resemblances, while homogeny (homology as applied to organs) is the warp, composed of the vertical, hereditary strands which connect animals with their ancestors and their successors.

The grander applications of analogy to the groups of mammals were first observed by Buffon in similar adaptations of animals evolving on different continents. In earlier studies of the marsupials of Australia Geoffroy St. Hilaire, De Blainville, and Richard Owen observed the remarkable analogies between the "families" into which these mammals are divided and the "orders" of the northern continents. Cope [1] also observed this grand mimicry of marsupial and placental orders.

More recently it has been discovered that the collective mammals of ancient South America, although of partly independent stock, in many ways mimic the collective mammals of North America in Cænozoic times.

[1] Cope, E. D., Origin of the Fittest. Essays on Evolution. 8vo, New York, 1887.

Again, the archaic, or Cretaceous placentals of North America and Europe, although alike marked by extremely low organization in certain characters, in other characters more or less closely imitate the radiations of higher groups and give us bear-like, cat-like, dog-like, and hyæna-like forms.

Connecting this principle with the laws of adaptive radiation, continental and local, we find that the radiations in different areas are more or less analogous with each other; that is, we discover many analogous radii or lines of adaptation, among other radii which are entirely dissimilar. When we come to compare the early evolution of the mammals in Africa, for example, we shall find that adaptation pursued entirely different lines from those pursued in Europe, Asia, and North America; so that when the African mammals finally entered Europe, after having undergone a long independent evolution of their own, they were entirely dissimilar and foreign in appearance to any with which they competed in Europe.

One of the most important advances of the past twenty years has been the clear recognition of this law of analogy and of the pitfalls which it constantly spread for the earlier students of mammals. It may be described as the very "will o' the wisp" of evolution, always tending to lead the student of descent astray.

The Law of Irreversibility of Evolution

A very frequent feature of divergent adaptation is the loss of parts as explained on p. 15, or the very profound modification of parts, as in the "tree phase," of the early life of the marsupials, in which two of the toes become syndactylous, or closely applied to each other. These lost parts are never reacquired, nor can such profound modifications of form and proportion be overcome; a specialized organ can never again become generalized, lost parts are irretrievable. It follows that while the conditions of life may be recurrent or reversible, the conditions of adaptive structure are not reversible. Hence the dictum of Dollo [1] that evolution, while frequently reversible in conditions of environment and adaptation, is irreversible in animal structure. Each part that is lost, like a tooth or a digit, narrows down the possibility of future plastic adaptation to new conditions. Nature often resorts to other remedies to repair her losses, namely, to *substitution of parts, or to change of function.*

Thus extreme specialization accompanied by the great enlargement of certain parts and the great reduction of other parts often places a mammal in a *cul de sac* of structure, where it is incapable of further modification to meet a new environment. This may become a cause of extinction.

[1] Dollo, Les Lois de l'Évolution. *Bull. Soc. Belge Géol., Paléont., Hydrol.*, Vol. VII, 1893, pp. 164–166.

III. Geographic or Space Distribution of Mammals

Zoögeography. — We have seen above that we owe to Buffon (p. 19 ff.) and Cuvier (p. 22 ff.) the beginnings of the fascinating study of geographic distribution in past and present times. Cuvier clearly saw that the mammals which we find at any point on the earth to-day may not have originated there but have had their homes or centers of origin at far distant points. It has since become more and more evident that only through palæontology can we connect the present distribution of mammals with their distribution in the past, and set forth a science of geographic distribution, or *zoögeography*, which will be in harmony with both sets of facts. The importance of this more thorough study of present and past geographic distribution was recognized by Alexander von Humboldt. The first exact attempt to compare the animals and plants of the present and past in a single region was that of Edward Forbes in his remarkable paper on the geological relations of the fauna and flora of the British Isles.[1] In this paper he attempts to distinguish those animals and plants which are native to the British Isles from the immigrants, and among the latter he attempts to trace the sources, or geographic centers from which they came.

Many of the principles of zoögeographic distribution were clearly understood by Darwin and set forth in "The Origin of Species" in the year 1859, and it is noteworthy that in the same year Philip Lutley Sclater[2] divided the world into six zoögeographic regions, as follows:

Neogæa	Nearctic,	Boreal Zone	North America
	Neotropical	Tropical Zone	South America
Palæogæa	Palæarctic	Boreal Zone	Europe and Asia
	Indian	Tropical Zone	Southern Asia
	Ethiopian	Tropical Zone	Africa
	Australian	Austral Zone	Australia

We observe that Sclater's was an *east* and *west* division, or a *new* and *old* world division, based on the lines of longitude rather than of latitude. Murray's "Geographical Distribution of Mammals," published in 1866, served to arouse further investigation of this subject.[3]

The six great regions of Sclater were subsequently adopted in their entirety by Alfred Russel Wallace in his great work of 1876, "Geographical Distribution of Animals . . ."[4] the first comprehensive attempt at this

[1] Forbes, E., On the Connection between the Distribution of the Existing Fauna and Flora of the British Isles with the Geological Changes which have affected their Area. *Mem. Geol. Surv.*, Vol. I, 1846.

[2] Sclater, P. L., On the General Geographical Distribution of the Members of the Class Aves. *Jour. Proc. Linn. Soc. (Zoöl.)*, Vol. II, p. 130 (1857), 1859.

[3] Murray, A., The Geographical Distribution of Mammals, London, 1866.

[4] Wallace, A. R., Geographical Distribution of Animals, with a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface, 2 vols. London, 1876.

study. The fundamental suggestion of Sclater to divide the world into eastern (Palæogæa) and western (Neogæa) divisions proved, however, to be entirely inconsistent with the facts of past and present distribution. Huxley as early as 1868 had proposed a northerly (Arctogæa) and southerly (Notogæa) division, and it became gradually apparent [1] that the six great regions should be grouped into larger *northern* and *southern* Realms. Sclater (1874), J. A. Allen (1878), W. T. Blanford (1890), and Alfred Newton (1893), along various lines contributed to the conclusion that there are three such great primary realms based on a *north* and *south* division, namely: *Arctogæa*, *Notogæa*, and *Neogæa*. The regions as embraced in these realms are clearly set forth in the accompanying table.

Realms	Regions	Geographic Boundaries
I. Arctogæa		
	Holarctic Region	Europe, Asia, and North America.
	Nearctic Region	North America north of Mexico.
	Palæarctic Region	Asia, north of the Himalayas, Europe, and Africa north of the Desert of Sahara.
	Ethiopian Region	Africa, south of the Sahara Desert.
	Oriental Region	Asia south of the Himalayas, including Sumatra, Java, Borneo, and the Philippines.
II. Notogæa		
	Australian Region	Australia.
III. Neogæa		
	Neotropical Region	South America.

This division into grand zoögeographic Realms and Regions broadly, or in a general way only, conforms to the facts of distribution of mammals in past and present times, and these divisions correspond with the *main* events during the Age of Mammals, but are not to be understood as being separated either by sharp or continuous barriers. For example, while Neogæa, embracing the single Neotropical Region of South America, was during the greater part of the Age of Mammals separate from the other Realms, it shows at the beginning unmistakable proof of connection both with Notogæa (Australia) and with Arctogæa (the northern hemisphere), and toward the close of this Age it shows the most positive evidence of renewed union with Arctogæa through a commingling of the North and South American faunas.

Realms. — Thus it appears that while these grand Realms were the main centers of the adaptive radiation of the orders of mammals, the orders were not confined to these realms, but during periods of land connection certain members strayed into adjacent realms; that each realm, therefore, contains a mingling of its original, or autochthonous types and its

[1] The history of opinion on this subject is fully set forth in Lydekker's invaluable work, A Geographical History of Mammals, 1896, chap. i. Additional interesting details are found in R. F. Scharff's History of the European Fauna (1899).

migrant, or derived types. Thus *Arctogæa*, containing the broadest and most highly diversified land areas of North America, Asia, Europe, and Africa, appears as the center in which twenty-one primitive and specialized orders of mammals radiated from each other. In the southern Realm of *Neogæa*, more restricted geographically, four or five orders of mammals enjoyed their chief radiation. During the larger part of the Age of Mammals Notogæa (Australia, New Zealand, and Tasmania), shut off by the sea from Arctogæa, witnessed the highly diversified radiation of the Marsupials and of the declining group of Monotremes.

Regions in the zoögeographical sense may be thought of as more restricted areas of adaptive radiation of mammals which have been isolated

Fig. 9. — Chief zoögeographic Realms and Regions of the world on the Sclater-Huxley system.

from each other for shorter periods either by climatic barriers, as in the case of the arctic conditions of the north, or by great physical barriers, such as masses of water or desert sands. Whereas the Realms are the centers in which orders originate, Regions in general are chiefly distinguished by the adaptive radiation of families of mammals. This, while broadly true, is not universally true, for the Ethiopian Region (Africa south of the Sahara) appears to have given birth during early Tertiary times to several orders of mammals, namely: Barytheria, Embrithopoda, Hyracoidea, Proboscidea, and perhaps the Sirenia and Cetacea. The two marine orders of mammals, last named, are also attributed to the hypothetical 'Atlantis,' or atlantic archipelago connecting Africa and South America (see J. W. Gregory, Eigenmann, and others).

It must be very clearly understood, therefore, that all the modern zoögeographic divisions, Realms, Regions, sub-Regions, etc., are chiefly

used for purposes of convenience, that they express the truths of geographic distribution in their grander outlines but not in their details.

In the shifting geographic and physiographic scenes of the enormously protracted Age of Mammals the lines of division are now sharpened by continental depression and separation, by isolation and insulation, and again blended by continental elevation or by the formation or renewal of migration routes, and by the opportunities, of which the mammals are prone to take immediate advantage, to extend their geographic range by migration.

Thus we shall see in past times the Nearctic and Palæarctic now blend into the Holarctic, and again separate more widely than at present. Again, we shall see the Ethiopian, Holarctic, and Neotropical blending far more closely than they do at present. In truth, *there can be no uniform system of past and present distribution*, as the present writer once fondly hoped. Every geologic Era, every Epoch, and even every Period has its own laws of distribution.

Migration Routes and Barriers

Checking the tendencies of mammals to migrate are inconspicuous barriers of many kinds in the living world and in animals themselves, as well as the more obvious and conspicuous physiographic and climatic barriers. Mountain chains, broad rivers, stretches of sea, of desert, or of forest, which freely facilitate the migration of some kinds of mammals and form absolute checks to the migration of other kinds, present barriers no more formidable than those indirectly brought about by certain degrees of moisture and of heat or cold. Thus "temperature zones" form barriers wherever they control the periods of reproduction.[1] Moisture may infest a country with insect pests, such as flies, ticks, and mosquitoes, which form as absolute a boundary to migration as a broad mass of water. Animals which are so specialized as to be restricted or confined to certain habitats may be said to impose their own barriers upon themselves.

Most barriers are ultimately traceable to changes in the greater and lesser land masses and their connections, caused by the elevation or subsidence of various parts of the earth. These changes both make and destroy land routes, and cause a series of changes in all physical conditions of climate, moisture or desiccation, of temperature, or heat and cold. The succession of faunas during the Miocene and Pliocene periods in Europe is positive proof of a succession of environments.

In this connection it is highly interesting to compare the stable continents of North America and Africa, which show relatively slight fluctuations of land and sea level during the Age of Mammals, with the highly unstable continent of Europe. During a considerable part of the Age of

[1] Merriam, C. H., The Geographical Distribution of Life in North America with Special Reference to the Mammalia. *Proc. Biol. Soc. Washington*, Vol. VII, April 13, 1892.

Mammals Europe is like a peninsula budding off from the western side of Asia or at times almost like an archipelago, so largely does the sea transgress its northern and southern borders. Its varying coastlines, its insular conditions, its archipelagic surfaces are to be followed in imagination in connection with the evolution of its mammalian fauna. Nevertheless the main trend of evolution and extinction in unstable Europe coincides with that in relatively stable North America.

IV. Geologic or Time Distribution of Mammals

Time divisions. — A host of questions turn upon the geologic, or *time* distribution of mammals, which is to be studied hand in hand with their geographic, or space distribution, as above described. The precise solution of all problems of origin and dispersal, or travel and migration of the different kinds of mammals, concluding finally with the most absorbing question of the center of origin and dispersal of the human race, turns upon the question of geologic time.

At present, from astronomical reckoning, we may all ascertain the time and readily fit all that is occurring in different parts of the world into the days, weeks, and months. In the past, however, in the geologic time divisions[1] which are known as Stages (*Étages*), Periods, and Epochs, we directly invert our present order of procedure, because we must first discover what is occurring in the different parts of the world, and from these occurrences we must deduce, estimate, and establish geologic time.

If the question is asked when did the Age of Reptiles close and the Age of Mammals begin, in France, in the Rocky Mountains, or in South America, the answer is sought not through the rocks, but through the fossils which they contain, or through a process of observation and reasoning which is known technically as *palæontological correlation.* When we compare all the fossil mammals which are known in the dawn of the Eocene in Europe, in North America, and South America, we are able to establish a *homotaxis* or general similitude in the life of these widely separated regions, and a *synchronism,* or general similitude in the time of these different regions. An exact synchronism is practically impossible of attainment, but approximate synchronism, or time correlation, is by no means beyond our reach, although often a vastly long and difficult undertaking.

The very title of this volume, "The Age of Mammals," implies the

[1] Comptes Rendus de la VIII^e Session, en France, Congrès Géologique International, Paris, 1900 (1901). This International Geological Congress ruled the following use of terms:

1. *Eras* = Palæozoic, Mesozoic, Cænozoic.
   (Cænozoic = Tertiary + Quaternary.)
2. *Periods* as Cambrian, Silurian, Cretaceous, etc.
3. *Epochs* = Eo . . ., Meso . . ., Neo . . ., as Eodevonian, Mesodevonian, Neodevonian, etc.
4. *Ages* = *Étages* = (Ages or Stages), as Astian, Bartonian, etc.
5. *Phases* = *Life Zones,* such as "zone à Cardiola," etc.

question of time, and it is one of our chief objects in this review of the history of the fossil mammals of the Old and New Worlds to use this history as a means of closely establishing similar divisions of past time in these two widely separated geographic regions.

Employing the suggestive terms of Louis Agassiz, the whole life history of the earth may be divided into Ages of Invertebrates, of Fishes, of Reptiles, of Mammals; the latter Age comes as the last episode before the final Age of Man. The Age of Mammals is technically known as the *Cœnozoic Era* (Age of Recent Life), a term which is partly equivalent to but has generally replaced the older term Tertiary, which signifies the third period in the history of life. The Cænozoic is subdivided into two Periods and six Epochs, as follows:

		Epochs
Cænozoic Era	Quaternary Period	Holocene, (from ὅλος, entire, καινός, recent), or recent time, characterized by the world-wide destruction and elimination of mammals through the agency of man.
		Pleistocene (from πλεῖστος, most, καινός, recent), a life period in which the majority of the recent forms of mammals appear and in which there occurs the last glacial period and a great natural extinction of earlier forms in all parts of the world.
	Tertiary Period	Pliocene (from πλείων, more, καινός, recent), a vast modernization of the mammals in which all the existing orders and families are known, as well as many of the existing genera, but few or no existing species.
		Miocene (from μείων, less, καινός, recent), an earlier stage of modernization, in which lived many mammals closely similar to existing forms.
		Oligocene (from ὀλίγος, little, καινός, recent), characterized by the appearance of many existing types of mammals and the gradual disappearance of many of the older types.
		Eocene (from ἠώς, dawn, καινός, recent), characterized by the first appearance of many of the ancestors of the modernized mammals and the gradual disappearance of many of the archaic types characteristic of the Age of Reptiles.

These grand time divisions of the Cænozoic are the work of the nineteenth century, and the incessant trend of discovery is to multiply time divisions and make them more minute. The work of the twentieth century is precise correlation. The ardent studies of the great French naturalists Lamarck, Alexandre Brongniart (1770–1847), Cuvier, and Deshayes in the early part of the nineteenth century, the golden age of palæontology in France, were accompanied by a growing realization of the vast stretches of geologic time as witnessed in the vast changes which have taken place in the animal life of the globe and in the enormous thickness of some of the sedimentary rocks which had been deposited even during this later or Tertiary Period. It became absolutely necessary to make divisions of the Tertiary; the threefold division was in the first instance due

to the monumental researches of Gérard Paul Deshayes (1795–1875) on the succession of the shells in the Paris Basin; he perceived that as we pass from the older and lower to the higher and more recent geological levels there is an increasing percentage of living types or species. To the threefold division discovered by Deshayes, Charles Lyell in 1833 applied the names *Eocene*, *Miocene*, and *Pliocene*. In 1854 Heinrich Ernst Beyrich (1815–1896) perceived that in many parts of Europe a fourth grand division existed between Eocene and Miocene times, for which he proposed the term *Oligocene*. Another step in this naming of the periods or *systèmes* was in 1839 when Lyell [1] proposed the term "Pleistocene" for the period succeeding the Pliocene and preceding the Recent or Holocene.

Students of fossil shells also took the leadership in further dividing the Age of Mammals into time periods by demonstrating that the epochs can be subdivided into stages, or *étages*. Thus the French invertebrate palæontologist, Alcide Dessalines d'Orbigny (1802–1857), divided the Eocene of France into a lower stage, or *Suessonian*, named from the deposits chiefly north of Paris, and an upper stage, or *Parisian*, named from the deposits around Paris. Successive proposals of D'Orbigny, Duméril, Mayer-Eymar, Suess, Depéret have finally led (1889) to the subdivision of all the Cænozoic periods into a large number of STAGES which receive their names from the geographical localities in which they are most typically represented in various parts of France, Belgium, Italy, and Sicily. It is now recognized that each of these stages represents a long period of time. These stages and their approximate parallels in North America are exhibited in the accompanying table.

Preliminary Correlation

		EUROPE	ASIA	NORTH AMERICA
PLIOCENE	Upper	SICILIAN	Siwaliks	'Loup River'
	Middle	ASTIAN	Siwaliks	Blanco
	Lower	PLAISANCIAN	Siwaliks	Thousand Creek Rattlesnake and Republican River
MIOCENE	Upper	PONTIAN	Manchhar	'Loup Fork' Madison Valley Clarendon
	Middle	VINDOBONIAN	Manchhar	Deep River Pawnee Buttes Mascall
	Lower	BURDIGALIAN	——	Arikaree 'Upper Harrison' Upper Rosebud

[1] Charles Lyell, Antiquity of Man, 1839, p. 6.

			Africa	
Oligocene	Upper	Aquitanian		Harrison (Lower) John Day White River (Upper)
	Middle	Stampian		White River (Middle) Brule Clays
	Lower	Sannoisian	Fayûm	White River (Base) Cypress Hills Pipestone Creek Chadron
Eocene	Upper	Ludian	Fayûm	Uinta (Upper and Middle) Washakie (Upper)
	Middle	Bartonian		Uinta (Lower) Washakie (Lower) Bridger (Upper)
		Lutetian		Bridger (Lower) Huerfano (Upper)
		Upper Ypresian		Bridger (Lower) Huerfano (Upper) Green River
	Lower	Lower Ypresian		Huerfano (Lower) Wind River Wasatch (Upper)
		Sparnacian (Upper Landenian of Belgium)		Wasatch (Lower)
		Upper Thanetian (=Cernaysian) (Lower Landenian of Belgium)		Torrejon Fort Union
	Basal	Lower Thanetian		Puerco Fort Union
Cretaceous Uppermost		Danian=Maestrichtian (Terrestrial) (Marine)		Hell Creek

Importance of Time Correlation

If we are eager to solve the great number and variety of most interesting questions still unsolved as to the source, origin, affiliation, migration, and extinction of the noble races of animals which passed across the stage of the northern hemisphere, or ancient *Holarctic Region*, during the Cænozoic Period, we must endeavor to use very exact methods of com-

parison, to establish so far as possible the homotaxis or the synchronism of the geological subdivisions of the Cænozoic in the New and Old Worlds, and to agree upon the limits which shall be assigned to the Eocene, Oligocene, Miocene, Pliocene, and Pleistocene Epochs and their stages.

It will certainly prove best that the grandly successive series of Tertiary horizons in France should be adopted as the *chief bases of time division*, partly because of their priority of description and definition, but chiefly because in France, owing to the instability of the continent above referred to, there is a remarkable alternation of fresh-water deposits containing remains of mammals and of marine deposits containing fossilized shells, the shells serving as time-keepers of the evolution going on in other parts of the world. Thus in France the evolution of mammals, or the vertebrate time scale, is checked off by the invertebrate time scale. As we shall see, the Lower Cænozoic of America from the base of the Eocene to the summit of the Oligocene offers us a much more complete life story than that of France; in fact, it is an unbroken historic chapter. The same is true of our Oligocene and to a somewhat less extent of our Miocene. But the mammal-bearing series is entirely fresh-water. Only during the late Miocene and Pliocene of Florida and in the little known Oligocene of New Jersey, do we discover an alternation of marine and fresh-water conditions such as occurs throughout the entire Cænozoic in France. In the Pliocene our country affords only a series of vistas of what was happening, while Europe offers a more commanding view.

If, therefore, France, Germany, Switzerland, and Italy furnish the initial basis for time standards, comparison with America will serve to check and amplify. Thus the final basis for time divisions of the Cænozoic will be *international*. There is every reason for the international usage of similar terms, both as to life forms and as to time stages. In these matters patriotism and provincialism naturally should have no weight; palæontology knows nothing of the divisions formed by the English Channel, the Rhine, nor the Atlantic; it does not recognize the superiority of an English system, a French, a German, or an American system, but like all its sister branches of science, in these times of absolute scientific good will, demands an international system. If approximate synchronism in the Epochs and Stages can be established, and the present volume is designed to bring together all the facts that can be assembled toward such synchronism, it will be very desirable to adopt uniform descriptive terms for the European and American geologic divisions.

Our first object is to show how far the Epochs or *Systèmes* of America and Europe can be synchronized and similar permanent limits be placed between them; our second object is to establish *Stages* as convenient divisions of each, in addition to the descriptive terms *Upper*, *Middle*, *Lower*, and *Basal*, which are respectively marked off in the natural geologic boundaries of the two continents. Of course the synchronizing of the stages and substages throughout will present greater difficulties and

may in some instances prove impossible, owing to the absolute independence of the movements of the earth and of the other physical phenomena which caused these stages in the Old and New Worlds. It is obvious that the overlapping in time of these minor periods of deposition would be the rule and that exact synchronism would be largely coincidence and therefore highly improbable; all that we can reasonably hope to establish in the near future is *approximate synchronism of the stages*. Ultimately the lines of time overlap may be determined.

Time Value of Fossils

During the Age of Mammals we should endeavor to establish *absolute time* in different parts of the world, like Greenwich standard time of to-day, not through measuring the thickness of the rocks but through using as our chronometers all the known forms that lived, plants, and vertebrate and invertebrate animals. The thickness of the rocks varies enormously, and is correspondingly deceptive. The fresh-water Oligocene rocks of the western plains, for example, are only 400 to 800 feet in thickness, while on the Pacific coast and in Italy marine rocks of the same age are 10 to 12,000 feet in thickness. The thickness of rocks is one of the means of estimating the total duration of the Age of Mammals, while the stages of evolution in animals and plants give us the punctuation points, as it were, or the means of keeping geologic time. It is true that during the Cænozoic Era the plants are comparatively stationary, and so are the amphibians, fishes, and reptiles, but the mammals are in a state of continuous and incessant change, and what gives them especial chronometric value is that the rate of change or of evolution is the same in many parts of the world at the same time. Even during the Age of Reptiles we may take advantage of the remarkably constant evolution of the herbivorous multituberculate gnawing mammals known as Plagiaulacidæ, surviving members of which are found in the Basal Eocene (Fig. 28). The grooves on the sides of the large cutting teeth of *Plagiaulax* and the cusps, or tubercles, on the grinding teeth are successively added with the precision of clock-work, while the number of premolars is diminishing. If we suppose the rate of evolution has been about the same, we can approximately calculate the intervals of deposition.[1]

	Age of Reptiles			Age of Mammals	
	Stonesfield	Purbeck	Laramie	Puerco	Cernaysian
Diminishing number of premolars	?	4–3	2	2–1	1
Increasing grooves on premolars	?	7–9	11–14	12–15	14
Increasing number of molar tubercles: outer; inner .	?	4 : 2	6 : 4	6 : 4	9 : 6

[1] See Osborn, H. F., The Rise of the Mammalia in North America. *Proc. Amer. Ass. Ad. Sci.*, 1894, pp. 188–227; and *Amer. Jour. Sci.*, Nov. and Dec., 1893.

Similarly the slow stages in the attainment of perfection in the grinding teeth of the Eocene horses are of great value as time-keepers; for example, in the molars of *Eohippus* and *Orohippus* we observe that in the lower levels a certain cusp is adumbrated in shadowy form; on a slightly higher level it is distinctly visible; on a still higher level it is fully grown. We do not observe any sudden breaks, but a series of minute gradations, always in the direction of adaptation, because it appears that these changes in the teeth, which Osborn has called "rectigradations," may be of the same kind as those to which Waagen applied the term "mutations" in observing shells of successive geological levels. Whenever a new character is thus gradually brought to perfection, the animal is assigned a new specific name; *Eohippus validus* becomes *Eohippus venticolus*, or *Orohippus ballardi* passes into *Orohippus progressus*. When a number of these new characters thus gradually assemble in different parts of the tooth series, or in the feet, we assign a new generic name: *Eohippus* becomes *Orohippus*, or *Orohippus* becomes *Epihippus*. The specific and generic names which were applied both in Europe and America to the Eocene horses by Owen, Cope, and Marsh were in every case defined by the presence of such slowly evolving new characters or groups of characters.

Now the time-keeping value of mammals lies in the fact that in Great Britain, in France, in Switzerland, in the Rocky Mountains, in short, wherever these inconspicuous but important 'rectigradations' are appearing, they arise at approximately the same rate and approximately in the same order even among animals which are widely separated geographically.

Close geologic synchronism, moreover, requires a comparison of the entire fauna and entire flora. The survival of a few primitive or arrested types may mislead, as in Australia, for example. Huxley [1] was somewhat doubtful of the time-keeping value of fossils; at least he thought the application might be overdone. He went so far as to say, "It is possible that similar, or even identical, faunæ and floræ in two different localities may be of extremely different ages, if the term 'age' is used in its proper chronological sense." Such a possibility as Huxley imagined has never been more than partly realized. Among the mammals as well as among the plants there is a constant progression which is, on the whole, a guide or index to synchroneity. This does not preclude such broad statements as the following: that the general aspect of modern Africa resembles that of Pliocene Europe.

Various Evidences of Synchronism and Homotaxis

When we attempt to compare what is going on in the Old and New Worlds during the enormously long time which is called the Age of Mam-

[1] Huxley, The Anniversary Address of the President. *Quart. Jour. Geol. Soc. London*, Vol. XXVI, 1870, pp. 29–64; Scientific Memoirs, Vol. III, p. 526.

mals we should not limit ourselves to mammals, but should appeal to as many classes of facts as possible, facts of climate, of geology, of physiography, of migration and colonization, and the rise, dominance, and decline of certain kinds of animals and plants.

In comparing the mammals of the two regions we look for the following tests:

1. *Presence of similar species.* — Those classic or time-honored bases of comparison in establishing percentages through the presence or absence of similar genera and species lead us to most interesting results, because they prove that the mammals of the Old and New Worlds were alternately brought together and separated. In other words, there was an alternating convergence and divergence of the faunas. The resemblances will first be very numerous and close, then there will come an estrangement when they will be very few, then the resemblances will suddenly increase again. It is obvious that only during the periods of faunal resemblance are we able to use the following or second method of comparison.

2. *Similar stages of evolution.* — This second method of comparison is based upon the similarity in the stages of development of like phyla of the mammals on the two continents, as expressed in the detailed changes in the grinding teeth (molars and premolars), in the numerical reduction of the digits, etc. For example, the different transformations of the premolars, or anterior grinding teeth in the horses, rhinoceroses, and tapirs during the Eocene and Oligocene Epochs afford very exact data for correlation purposes.

3. *Simultaneous appearance or introduction of new mammals.* — The sudden appearance both in the Old and New Worlds of mammals which have no known ancestors in lower horizons and have apparently originated elsewhere is of great value in correlation. These coincident immigrations from unknown northern regions (Eurasia) or from southern regions (Africa) in several cases give us very exact datum points; for example, certain kinds of modernized mammals simultaneously appear in Europe and in North America in Lower Eocene and again in Oligocene times.

4. *Intermigration periods.* — These periods are those in which conspicuous interchanges of mammals took place, as between North and South America in the Pliocene. The horse (*Equus*) being unquestionably derived from North America, its earliest appearance in North America must antedate its first appearance in South America.

5. *Predominance of certain kinds of mammals.* — Many related families of mammals seem to go through a cycle of gradual ascent until they attain a stage of world-wide predominance at about the same periods. For example, the climax of the odd-toed ungulates (Perissodactyla) is in the Middle and Upper Eocene of Europe and North America, while the climax of the even-toed ungulates (Artiodactyla) comes at a later period.

6. *Extinction periods of certain mammals.* — World-wide predominance has its counterpart in the world-wide disappearance or extinction of certain forms, correlated with grand geologic and physiographic changes. An example of this kind is the very general extinction of browsing types of Herbivora during the Oligocene. Among rodents, the beaver-like *Steneofiber* disappears at the same time both in Europe and North America, or is replaced by modified forms.

This general comparison of the evolution stages of the Old World and the New World will naturally become precise and final only after the time in the Old-World stages and in the New has been separately established and defined. Thus there are correlation problems, as follows:

European or Eurasiatic Correlation.
American Correlation.
American and Eurasiatic Correlation.
North and South American Correlation.

When these four broad problems of American-Asiatic-European-African correlation and of the broader New and Old World correlation are worked out we shall be able to establish a complete and very accurate geologic time scale for the entire Age of Mammals, and to speak with precision regarding the time of successive migrations, appearances, and extinctions. It is even possible that we shall be able in the New and Old World to employ the same stages or subdivisions of the Epochs of time.

Geologic Formations and Life Zones

The earth's crust is made up of a vast series of separate deposits which are technically known as 'formations.' The formation is the *geologic unit.* It may vary in thickness or in extent of geographic distribution; it may be laid down in many ways, such as by the transporting power of water or of wind or through falls of volcanic ash, but it is of the essence of a 'formation' that the conditions of deposition remain more or less uniform; when the conditions change, as from fresh-water to marine, for example, we pass into a new formation.

If animal remains are varied in the formation, we may select among the number a very conspicuous or abundant or unique mammal as especially distinctive of the whole formation or of a certain level in the formation as marking off a *life zone.* The word 'beds' previously used in a similar sense is liable to cause confusion because it has also been applied to geologic formations. It is clear that while the geologic formation may be limited in extent, the *life zone,* owing to the wider geographic range of the mammal from which it takes its name, is not limited, but may be found elsewhere.

For example, in southwestern Wyoming there is a very thick, more or less uniform deposit of volcanic ash, or tuff, which has been named the

Bridger Formation, from its proximity to the famous old Fort Bridger.[1] The entire formation is 1800 feet in thickness. The upper half of it is distinguished by the sudden appearance of a very large and distinctive quadruped, *Uintatherium*, named after the adjoining range of Uintah Mountains, which are on the boundary between Wyoming and Utah. This animal is so very distinctive that we may speak of the Upper half of the Bridger formation as the Uintatherium Zone. One hundred miles east of the Bridger is a deposit known as the Washakie, and in the lower half of this we find the same quadruped, *Uintatherium*, very abundant and characteristic. Thus the Lower Washakie is also in the *Uintatherium Zone*. From the presence not only of *Uintatherium* but many other animals in common we are able to correlate these two formations, as follows:

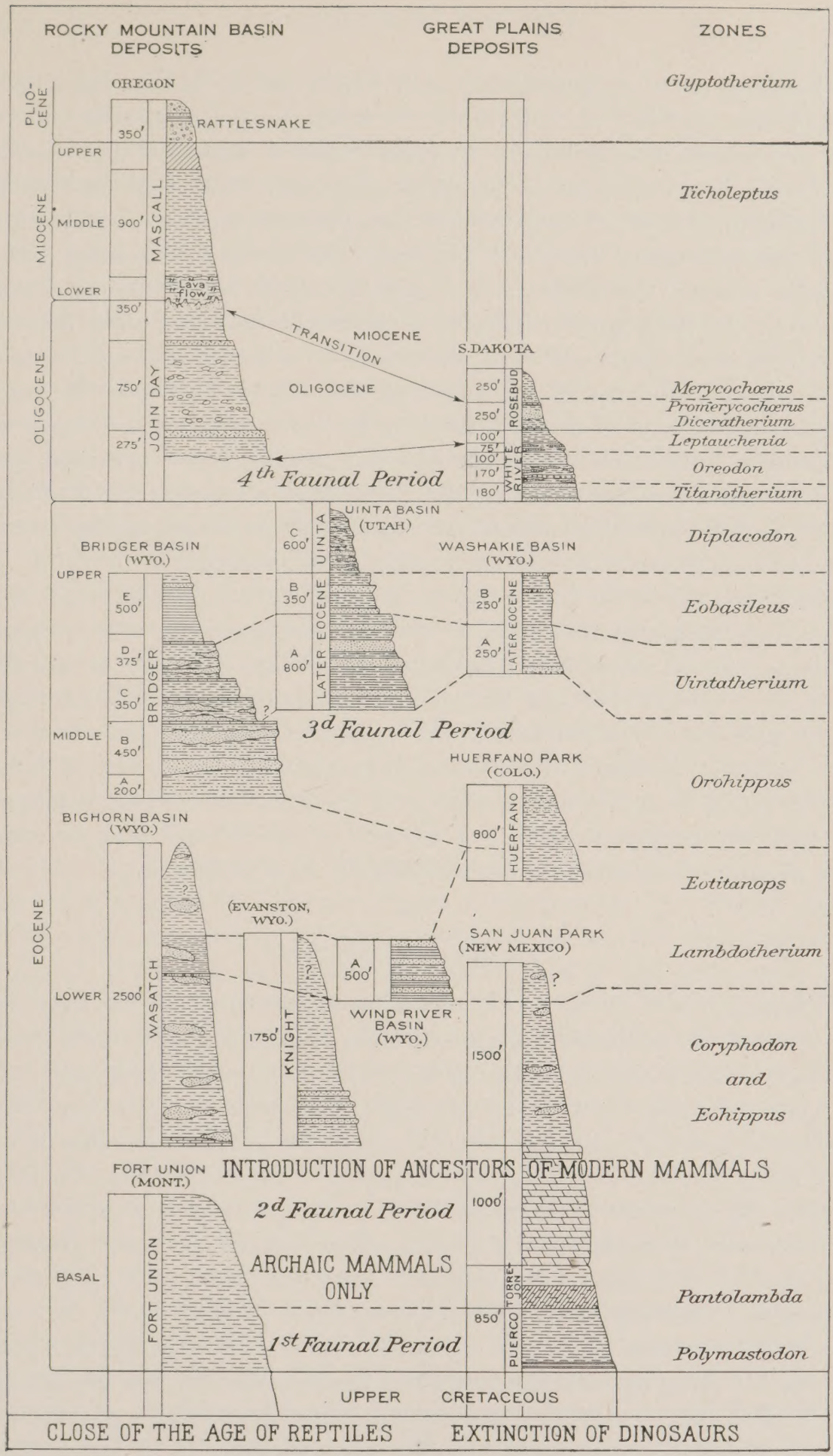
Formations				Zones
		Upper Washakie	=	Eobasileus zone
Upper Bridger	=	Lower Washakie	=	Uintatherium zone
Lower Bridger	=			Orohippus zone

This single example illustrates how all fossil-bearing formations may be correlated with each other where they contain similar life zones. This furnishes a simple key to the elaborate correlations which the reader will find in the later pages of this work. The above is a striking example of an overlapping in time; that is, while the upper half of the Bridger Formation was being deposited, the deposition of its more or less distant neighbor, the Washakie Formation, began. In this case the two formations happened to be somewhat similar in their rock composition, both being composed of volcanic ash; but another *Uintatherium* life zone might be found in a formation of river sand or clay. Thus the life zone enables us to synchronize geological formations of many different kinds which may be widely distributed geographically, and may vary greatly in thickness.

It is obvious that the correlation of innumerable fossil-bearing formations of the Old and New World respectively can be made much closer and more exact than the correlation of the Old and New World combined; yet the method of investigation is in each case the same. It should be based on:

1. Comparisons of animals of similar mutative, specific, and generic stages.
2. Evidences of similar local evolution.
3. Dominance or scarcity of similar animals in the fauna as a whole.
4. Diminution, disappearance, or apparent extinction of similar forms.
5. First appearance of similar forms, apparently by migration or invasion from some other region.

[1] See Osborn, H. F., pp. 50 ff., Cenozoic Mammal Horizons of Western North America. *U.S. Geol. Surv., Bull.* 361, 1909.



By permission of the U. S. Geological Survey.

FIG. 10. — Successive and overlapping Formations of the Rocky Mountain Region in Eocene and Oligocene times. Key to the series of *scale sections* in the subsequent pages; all the sections are drawn to same scale. The horizontal dotted lines indicate the boundaries of similar Life Zones.

Sources of error in correlation. — Evidence of these five kinds as the basis of the correlation of formations contains several sources of error. First, we should always be on our guard against imperfections in records and should keep in mind the possible presence, while a given formation was being deposited, of mammals which perhaps escaped fossilization or whose fossil remains have not yet been discovered. We must not too hurriedly assume the absence of a mammal from an entire continent or even from the geographic region of a certain formation simply because it has not yet been discovered in that formation. Many mammals long considered absent from the entire American Eocene, for example, the peculiar armadillo-like forms of South America, have recently been discovered in the Bridger Formation above mentioned. Again, some mammals living near the larger streams or along the shore lines are much more apt to be caught and entombed in certain formations than others living at a distance, in the forests or out on the uplands, for example.

Most formations are limited in geographic extent, and we must always keep in our imagination the life of the vast outside areas which were also thickly populated, with their differences of habitat, of longitude, or eastern and western distribution, of latitude, or northern and southern distribution, of altitude, or vertical distribution, such as on mountain ranges and in the valleys; in short, there were always in past times such differences of distribution as exist among mammals to-day, which render it improbable that the restricted area of a given 'formation' will give us an adequate picture of the entire contemporary life of a continent.

Progressive Correlation

European Correlations. — The foundation for the correlation of European formations with each other naturally began with the early work of Cuvier and advanced with the progress of mammalian palæontology on the continent. In France, Gervais ('59, '69), Gaudry ('62, '73, '78, '86, '88, etc.), Filhol ('77, '79, '81, '88, '91), Lemoine ('78, '80, '82, '85, '87, '88), Boule ('83, '88, '93, '96, etc.), and especially Depéret ('87, '90, '92, '93, '00, '05, '06) have successively described typical horizons or formations and the mammals characteristic of them. Parallels between the formations of England and France were early set forth by Owen ('60), followed by Sir Joseph Prestwich ('88), and William Boyd Dawkins ('80, '94). Parallels with Germany have been especially treated by Von Zittel, Schlosser ('88, '83–'97, '90, '95, '02), and Depéret ('85, '87, '90, '92, '93, '05, '06, etc.).[1]

The first step in correlation through faunal parallelism, or similar life zones, is naturally to assemble as full a list as possible of the characteristic species and genera of mammals. Valuable tables of such European faunal parallels are those given by Von Zittel in his great *Handbuch der*

[1] Principal titles are given in the Bibliography.

Palæontologie (1876–1893). Full and more precise lists of the European mammals characteristic of different formations or horizons are those assembled by Schlosser (1887–1890). The *Literaturbericht* (1883–1897) of the same author, a complete review of the literature of mammalian palæontology for the fourteen years indicated, is a mine of wealth for an investigation of this kind. Up to 1896, however, there still existed no satisfactory correlation of all the Old World horizons with each other, and it was obvious that a unified Old World system was absolutely necessary as a starting-point for exact comparison with the formations of the New World. Realizing that an acceptable working basis could only be secured by coöperation, Osborn drew up in 1897 a *Trial Sheet of the Typical and Homotaxial Tertiary Horizons of Europe* and circulated it for criticism and suggestion. Invaluable corrections were received, especially from the author's friends Gaudry, Von Zittel, Schlosser, Pavlow, Boule, Lydekker, and Depéret. The corrections were embodied in a *Second Trial Sheet* (April 15, 1898), which was used for further personal investigation and discussion with the above-named palæontologists, also with Lepsius of Darmstadt and Forsyth Major of the British Museum. A *Third Trial Sheet*, issued in 1900, was more accurate than its predecessors, but still lacked the desired exactness and fullness. The general state of knowledge in 1900 was brought together in the author's paper, "Correlation between Tertiary Mammal Horizons of Europe and America." [1] In June, 1905, there began in the *Comptes Rendus de l'Académie des Sciences* the epochal series of papers by Depéret entitled *L'évolution des Mammifères tertiaires; importance des migrations*. These papers covered with the desired fullness and precision the subject of the correlation of all the mammal-bearing formations of Europe, and moreover treated briefly and with great precision the succession of mammalian life in Europe, and the supposed migrations between the continents of the main land masses of Europe, Asia, Africa, and North America. Depéret's life zones and faunistic subdivisions of the Old World are adopted throughout the present volume as the standard for comparison with the New World. His correlation of formations is graphically expressed in a full series of maps. (See Figs. 26, 50, etc.)

American Correlation. — The chronological correlation of American mammal-bearing formations with each other opened in a very promising way through the exact methods which characterized even the early observations of the geologist Hayden and the palæontologist Leidy on the geologic formations of our Great Plains. Naturally errors crept into such a rich and new field, where many formations were so similar to each other in external appearance, and in a period of geologic thought which preceded

[1] Osborn, H. F., Correlation between Tertiary Mammal Horizons of Europe and America; An Introduction to the more Exact Investigation of Tertiary Zoögeography; Preliminary Study with Third Trial Sheet. *Ann. New York Acad. Sci.*, Vol. XIII, no. 1, July 21, 1900, pp. 1–64; and, Corrélation des horizons de mammifères tertiaires en Europe et en Amérique. *C. R. 8^e Cong. géol. intern.*, 1900, pp. 357–363.

a clear separation of the Oligocene, Miocene, and Pliocene faunas, but we cannot repress our admiration for the admirable attempts at precision on the part of Hayden and Leidy whereby Oligocene and Miocene mammalian faunas were separated off into six successive faunistic stages indicated by the letters A, B, C, D, E, and F.

Unfortunately this standard was not followed, and slow progress was made for many years, owing to very loose methods of collecting fossils for purely anatomical and descriptive purposes without closely recording geologic levels and life zones. Nevertheless considerable advance was made in the successive writings [1] of Cope (1879, 1884), Marsh (1877), Scott (1887, 1893), W. B. Clark (1891, 1896), Dall, (1896, 1897), Wortman (1893), Osborn (1897, 1898, 1900).

In the survey (1898) of the Middle Eocene Washakie Basin, Osborn and McMaster prepared the first geologic section which recorded the 'levels' on which different species of mammals were found.[2] The starting-point of the admirable precision of recent work was Hatcher's survey between 1886 and 1888 of the Lower Oligocene of the Great Plains, summed up in his paper, "The Titanotherium Beds," [3] in which he exactly described the stratigraphy, the geographic distribution, and the division of the *Titanotherium Zone* into Lower, Middle, and Upper levels. This was followed in 1893 by Wortman's paper "On the Divisions of the White River or Lower Miocene of Dakota," [4] which treated precisely the succession of mammals in the entire White River formation, now considered of Oligocene Age. In 1899 all the formations both of the mountain region and of the Great Plains of the West were for the first time accurately reviewed and compared by Matthew in his important paper, "A Provisional Classification of the Fresh-Water Tertiary of the West." [4] This paper was accompanied by a discussion of all the preceding work of correlation, by a review of all the principal formations then known, and by a complete faunal list of the species of mammals hitherto described, the first which had appeared subsequent to Leidy's great list published in 1869, thirty years previously.

The next review of the American life succession during the Age of Mammals is that of Osborn ('09), entitled "Cenozoic Mammal Horizons of Western North America." [4] This comprehensive paper, accompanied by "Faunal Lists of the Tertiary Mammalia of the West," by W. D. Matthew, forms the American basis of the present volume.

American and European Correlation. — This broader study has also advanced step by step, beginning with the comparisons made by Leidy,

[1] Principal titles are given in the Bibliography.

[2] McMaster, J. B., Stratigraphical Report upon the Bridger Beds in the Washakie Basin, Wyoming Territory, accompanied by profiles of three sections. In Osborn, H. F., A Memoir upon *Loxolophodon* and *Uintatherium*, two Genera of the Suborder Dinocerata. *Contrib. E. M. Mus. Geol. Arch.*, College of New Jersey [Princeton], Vol. I, 1881, pp. 1–54.

[3] Hatcher, J. B., The Titanotherium Beds. *Amer. Natural.*, March 1, 1893. pp. 204–221.

[4] For reference see Bibliography.

and has aroused the interest of all mammalian palæontologists in turn, including especially[1] Cope (1879, 1884), Filhol (1885), Marsh (1891), Scott (1888, 1889, 1894), and Osborn (1900, 1909). Especially interesting historically are Cope's first comprehensive papers, "The Relations of the Horizons of Extinct Vertebrata of Europe and North America" (1879),[2] "The Horizontal Relations of the North American Tertiaries with those of Europe" (1883),[3] compared with Filhol's *Critique* of these papers (1885). The most comprehensive recent paper is W. H. Dall's "A Table of the North American Tertiary Horizons correlated with one another and with those of Western Europe; with Annotations" (1898).[4] Dall's attention is especially directed to the southeastern portions of the United States, particularly Florida, where an alternation of marine and fresh-water formations with vertebrate and invertebrate life zones affords a very direct method of correlation with the European geological stages, which are notably distinguished by the alternation of marine and fresh-water conditions.[5]

Geological Formations as a Record of Environments

Our knowledge of what may be called the *procession of environments* in different parts of the world during the Age of Mammals is derived from three sources. First and foremost, from the structure of the animals themselves, which fairly mirrors the habitat in which they lived; second, from the impressions of plants which the rocks may contain; third, from the nature of the rocks in which the fossil remains are found entombed. These three kinds of evidence give us as complete a picture of the environment as we can ever hope to obtain, and they must be studied together. They give us a vista of the succession of the meteorologic or climatic phases of the period, of the general passage from warmer to cooler temperatures, from moister to drier conditions. We are enabled to restore physiographic conditions by separating the animals which naturally inhabit well-watered forests, lowlands, and rivers from those naturally frequenting plains and uplands, by separating those adapted to softer ground from those adapted to dry, partially arid plains, and by adding to this information that derived from evidences of successive fluviatile, flood plain, and aerial or æolian deposits. Therefore the examination of the rocks in which mammals are contained is little less important and interesting than the examination of the fossils themselves; the two studies should go hand in hand.

Beside the examination of the rocks another feature of geologic study which dovetails with the palæontologic is the exact and precise record-

[1] Principal titles are given in Bibliography.

[2] *U.S. Geol.* and *Geog. Surv. Terr. Bull.*, Vol. V, no. 1, 1879.

[3] Cope, E. D., Section 2 of The Vertebrata of the Tertiary Formations of the West, Book I, 1883, pp. 21–45.

[4] *U.S. Geol. Surv.*, 18th *Ann. Rept.*, 1896–1897.

[5] See Dall, Geological Results of the Study of the Tertiary Fauna of Florida, 1886–1903. *Trans. Wagner Free Inst. Sci. Phila.*, Vol. III, Pt. 6, 1903, pp. 1541–1620.

ing of levels. In strata like those of our American Oligocene, where deposition has been extremely slow, every foot of level may mark a long period of time; fifteen or twenty feet, or even less, may mark a time during which one species passed by mutation into another.

Fig. 11. — Chief areas of deposition in the Cænozoic of North America: black = littoral depositions of the Atlantic and the Pacific coasts; dotted = 'continental' formations of the Great Plains and of the Mountain Regions. After W. B. Scott.

This naturally introduces us to a closer examination of geologic formations of various kinds.

As shown above, while the geologic unit is the "formation," "life zones" may occur in formations totally differing in thickness, in the kind of rock, in geographic extent, in mode of deposition. These largely geologic data are, however, of constant service to the palæontologist as part of the record of the past conditions under which the animals lived.

The map of North America on page 54 illustrates clearly the two great divisions in the kinds of formations, namely, the *border areas* of *marine, estuarine,* and *fluvio-marine* deposition of formations (indicated in black) and the *central areas* of *continental* deposition (indicated in dots). Connected with this distribution is naturally the *power* which transported the sediments, whether of the sea or in inlets of the sea, whether of streams or rivers, or even of the wind. Sorted as to the *transporting power,* the various kinds of formations in which fossil remains of mammals occur are as follows:

1. *Marine.* Beneath the ocean or along its margins. Such formations occasionally contain the remains of land and freshwater mammals, mingled with those of marine mammals and shells. 2. *Estuarine.* Brackish water deposits along the inlets of seas and at river mouths; also indicated by the remains of animals. 3. *Fluviatile.* Freshwater sediments deposited in river channels or bays, at the mouths of streams, or in torrent fans. 4. *Lacustrine.* Freshwater deposits borne into lakes by rivers or streams, which beyond the coarser entrance areas may be of the finest grain and become evenly stratified through periodic sedimentation. 5. *Flood plain or overflow deposits.* Through periodic overflow, as of the Mississippi or the Nile. Vast stretches of country flooded with muddy water, which subsiding may also leave a stratified sedimentation. Very characteristic of the Middle Tertiary of North America. 6. *Lagoon deposits.* In abandoned river channels and shallow lakes which through evaporation may collect gypsum and other salts. Very frequent in the Cænozoic of France. 7. *Æolian or aerial deposits.* Transported by the wind on dryland surfaces, usually fine non-stratified sands and dust, always lacking the regular horizontal lines which may characterize lacustrine and flood-plain deposits. Frequent in the later Cænozoic of North America. 8. *Cave deposits.* Bones of animals living in caves, fallen or dragged into them, inclosed with other fine sediments. Where over-abundant they may consolidate into a "phosphorite" or phosphate deposit. Frequent in the Pleistocene of North America and Europe. 9. *Fissure deposits.* Bones accumulated in the same manner as in caves, or by wind or water action, in fissures of the rock, more or less consolidated, also sometimes forming "phosphorites." Frequent in the Cænozoic of Europe, as the famous fissure deposits of Egerkingen, of Lissieu, of Quercy.

The remains of fossil mammals may be deposited under any of the above conditions and thus occur in formations of many kinds. The least perfectly preserved are those washed along with coarse pebbles and gravels, while the most perfect as a rule are those found in the fine sediments of still water, of æolian dust, of asphaltum, or of volcanic ash.

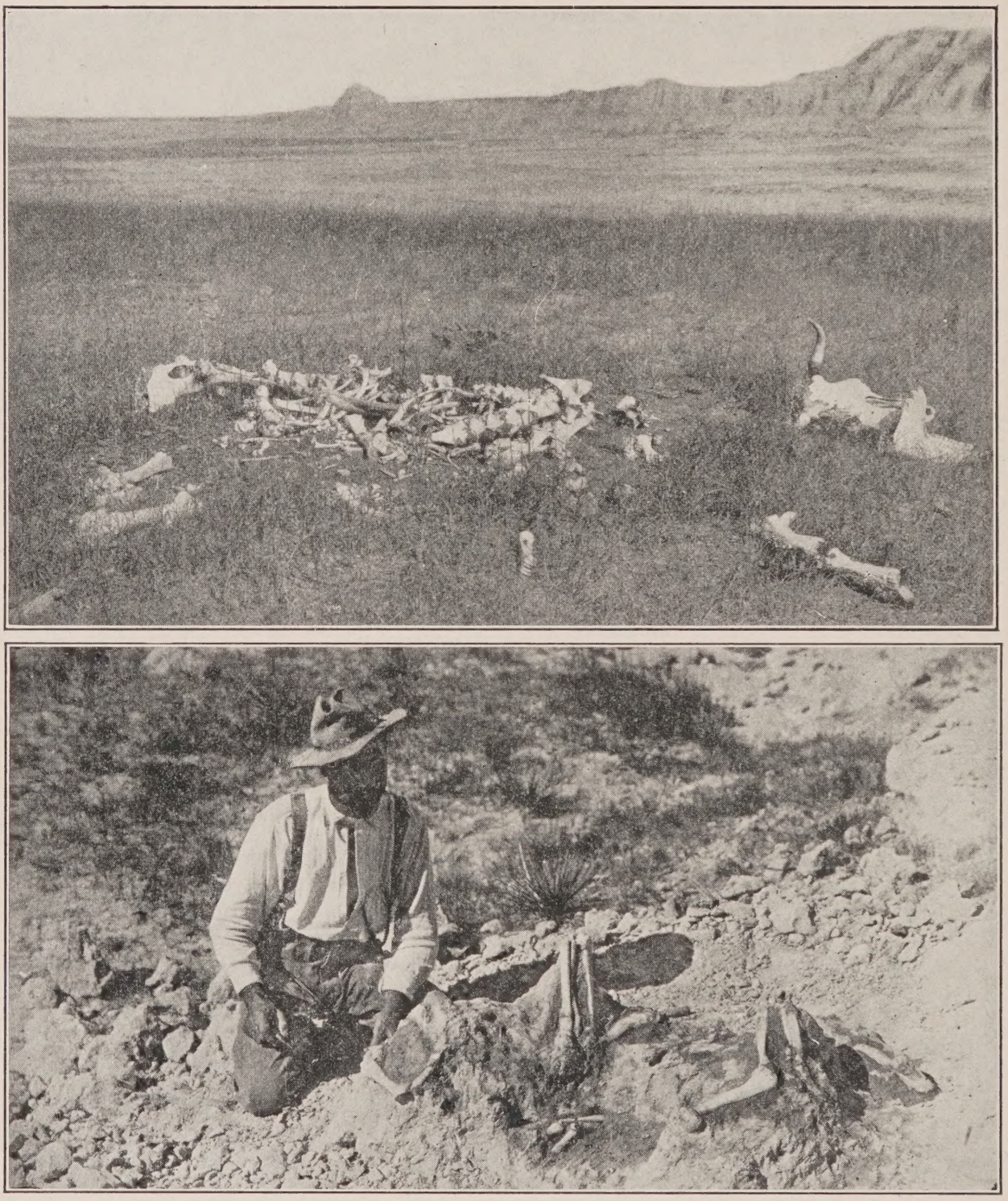


Fig. 12. — The imbedding of skeletons in æolian, or wind-drift deposits. Above: Recent times. Partially imbedded skeleton of an ox on the plains of South Dakota. Below: Miocene times. Partially exhumed skeleton of the fossil forest horse, *Hypohippus*, on the plains of Colorado.

The chief kinds of mammal-bearing rocks, that is, sorted as to *mineral composition*, are as follows:

1. *Conglomerates* (*"Conglomérats," "Konglomerate"*). Composed of weather-worn pebbles, gravels, and sands. They are evidence either of advancing or retreating shore lines of the sea or of river channels, or mountain streams where they spread upon the plains. 'Mud-ball' conglomerates are rather common in the western tertiaries. On the old sea borders of Eocene France we find the *Gravier*

marin de Cernay, de Meudon. In the great Oligocene Bad Lands of South Dakota it is most interesting to find the coarser sediments of a 'river channel' traversing a fine 'overflow' deposit, each containing its characteristic forms of mammalian life. Both in the deposits of the mountain regions and plains regions of the western United States great and small areas of these sediments occur containing either weatherworn or often battered fossils. 2. *Sandstones* (*"Grès," "Sandsteine"*). Composed chiefly of quartz sand or sometimes of feldspar grains (arkose sandstones), associated with deposits of volcanic origin, as in the Bridger Formation. Sandstones, due to sea and river action, naturally cover wider areas than the coarser conglomerates, which they often adjoin, because they display the transporting power of slower water action or higher wind action, as in deserts. Characteristic of late Pleistocene and Glacial times. 3. *Shales* (*"Argile schisteuse," "Schieferthon"*). Chiefly fine mud sediments, deposited in still or comparatively still water and exhibiting more or less perfect horizontal or oblique cleavage or lamination. Often contain beautifully preserved leaves and remains of fossil fishes, as the *Green River Shales.* Rarely contain remains of mammals. 4. *Clays* (*"Argile," "limon," "Thon"*). Due to river, flood plain, or deep water action, these are uniformly fine sediments, typically of continental origin, in large part a consolidated loess. The true "plastic clay" or *argile plastique* is mostly of marine origin and results from the final decomposition of feldspar. The famous *London Clay,* containing *Hyracotherium,* is an estuarine formation. 5. *Loess* (*"Loess"* in French and German). Characteristic of late Pleistocene and Glacial times. An unconsolidated, fine, porous, silicious silt, deposited on river flood plains, in back waters, and by the agency of the wind on dryland surfaces and (according to some authors) as glacial mud. Water-borne and wind-borne loess are hard to distinguish; some loess is of joint origin. In some regions loess is composed of volcanic ash more or less altered by weather and river erosion. Where of flood plain origin it may show horizontal color banding, due to seasonal floods, or in æolian loess to the direction of prevalent winds. A partially consolidated loess would be commonly called a clay; when further consolidated, a shale. The most famous loess deposit is the Pampean formation of Argentina, rich in mammals. 6. *Volcanic ash and tuff* (*"Tufs," "Tuff"*). The great constituent of the Mountain Basin formations of North America. Composed of volcanic ejecta, containing many feldspathic particles. Where wind-borne, the ash resembles loess; where water-borne, volcanic ash forms tuffs. Examples are large parts of the Bridger, Wind River, and other mountain basin formations of North America. 7. *Lignites* (*"Lignites," "Braunkohle"*). Rare as a Cænozoic formation in America, common in the Eocene of Europe, as the *Lignites du Soissonais, de la Débruge, de Cadibona.* 8. *Gypsum* (*"Gypse," "Gyps"*). Formed by evaporation of lagoons. Afford an invaluable indication of climatic conditions. The most famous deposit of the kind is the Upper Eocene *Gypse de Montmartre,* near Paris. 9. *Limestones* (*"Calcaire," "Kalk"*). Limestones, as the *Calcaire grossier* of the Upper Eocene of France, are chiefly calcareous (carbonate of lime), sometimes of organic origin, or formed by the accumulation of shells; sometimes by deposition from water holding lime in solution. Travertines are calcareous deposits formed from hot springs. 10. *Marls* (*"Marnes," "Mergel"*). Loose or unconsolidated deposits of earth, of lime, of shells, etc., rich in organic matter. Phosphate Beds are marls or other formations rich in phosphate of lime, such as those of South Carolina; they are littoral and estuarine in

origin and may contain the intermingled remains of land and sea animals. 11. *Phosphorites* (phosphate of lime) (*"Phosphorites," "Phosphorit"*). Also of organic origin, directly or indirectly derived from the hard parts of animals, or from the excrements of animals. 12. *Asphalt or asphaltum* (*"Asphalte," "Asphalt."*) The residuum of pitch lakes left by the evaporation of petroleum springs. A remarkable asphaltum deposit (Rancho La Brea, see Fig. 205) has recently been found in the Pleistocene of southern California, containing a rich variety of mammals in remarkable preservation. 13. *Breccias* (*"Brèche," "Breccia"*). Formed by the filling in of bones and gravels cemented together by calcareous waters.

V. Duration of the Age of Mammals

How long was the Age of Mammals? How many years ago did it begin? How may we find out? If we remark, for example, that *Eohippus*, the first stage in the development of the horse, was an animal which lived about three millions of years ago, our hearer looks incredulous and has a perfect right to ask, What are your grounds for assigning such an enormously long period of time? There are a great many ways of estimating geologic time, all of which either depend on the comparison of past processes with present processes of earth formation, or make an appeal to astronomic data, such as the procession of the eclipses, the eccentricity of the earth's orbit, or the consolidation of the earth's crust and the period necessary for cooling sufficiently to admit of life.

A vast period. — Whatever method of calculation we adopt, a glance at the accompanying diagram shows that the Age of Mammals, while vastly long in itself, was *relatively* short as compared with all the life periods which preceded it; it was estimated by Dana in 1874 as occupying only one-sixteenth of the whole life period, by Wallace in 1895 as occupying one-twentieth of the whole life period. Each of these Ages represents a vast interval, as attested both by the great geographic changes which occurred in them, by the great mountain chains which were thrown up and then completely reduced to the general level, by the enormous thickness of the sedimentary deposits which were laid down on land and sea, recently estimated at a total of 265,000 feet or upwards of 50 miles (Sollas, 1900), or 335,800 feet (Sollas, 1909), and still more perhaps by the great changes in the animal and plant life which are recorded in the fossils.[1]

Mountain births. — Biologists from Darwin to the present time have demanded long periods for these evolutionary changes and for the Age of Mammals itself. As a measure of the lapse of time the comparison of the great advance in size and structure between the Eocene *Eohippus* and the existing horse (*Equus*) (Fig. 14) is perhaps less impressive than a review of the great mountain births which occurred during the Age of Mammals.

The Rocky Mountains, it is true, began their elevation during the close

[1] See Poulton, 1896, A Contribution to the Discussion of the Age of the Earth, Essays on Evolution, 1908, p. 15.

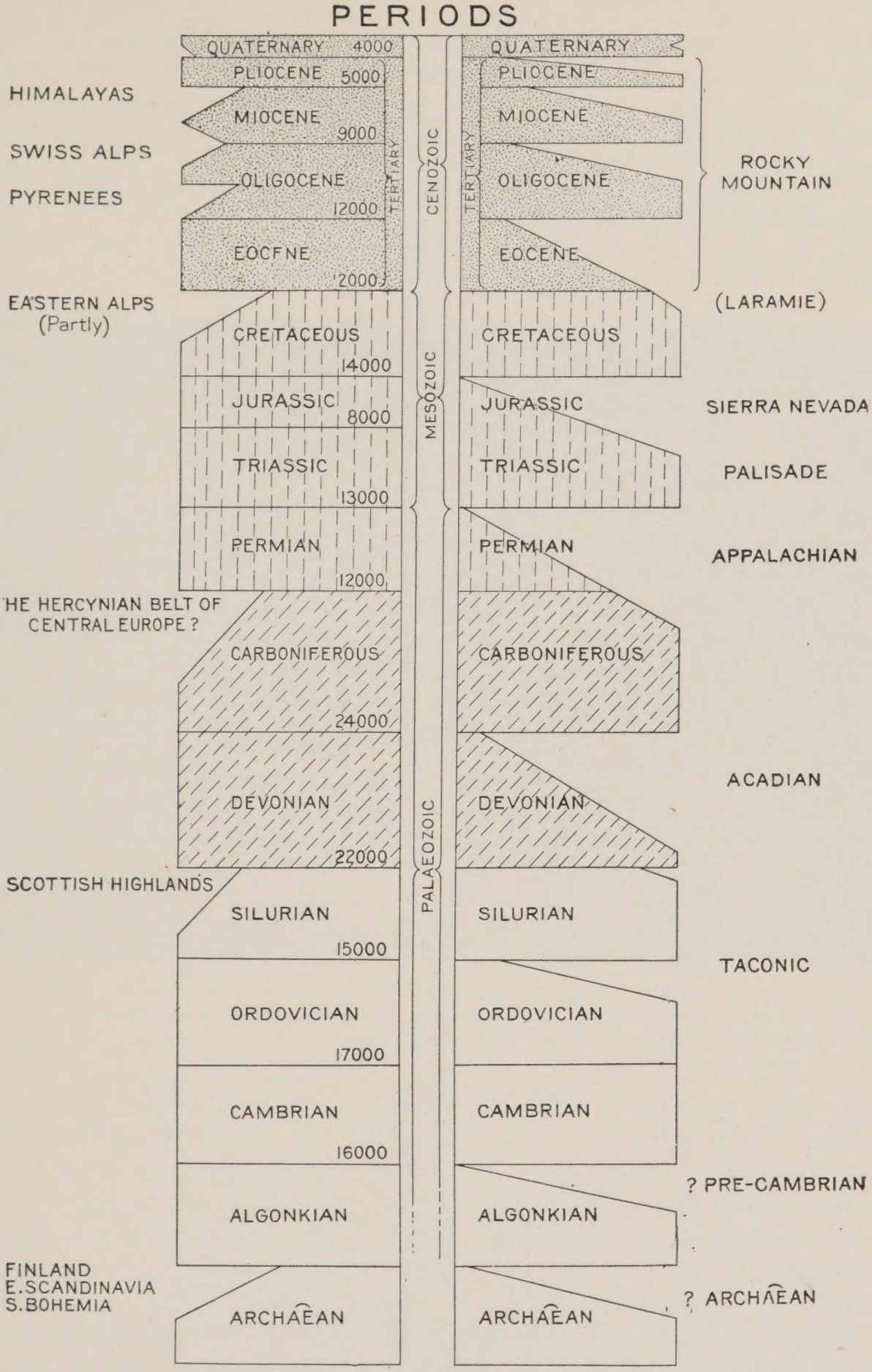


FIG. 13. — A diagram showing what the total thickness of the earth's crust would be if all the surface deposits since the time of the first appearance of life had accumulated on top of each other. Age of Mammals = dots. Age of Reptiles = vertical lines. Age of Amphibians and Fishes = oblique lines. The births of American and Eurasiatic mountain systems are indicated by incisions of the right and left hand columns respectively.

of the Age of Reptiles; they had only attained a height of four or five thousand feet when the Age of Mammals commenced; they continued to rise during the entire period. But consider the map of Europe and Asia at the beginning of Eocene time and realize that the great mountain systems of the Pyrenees, the Alps, and the Himalayas were still unborn, level surfaces in fact, partly washed by the sea. As shown in the diagram, the birth of the Pyrenees was at the beginning of the Oligocene. At this time Switzerland was still a comparatively level plain, and not until

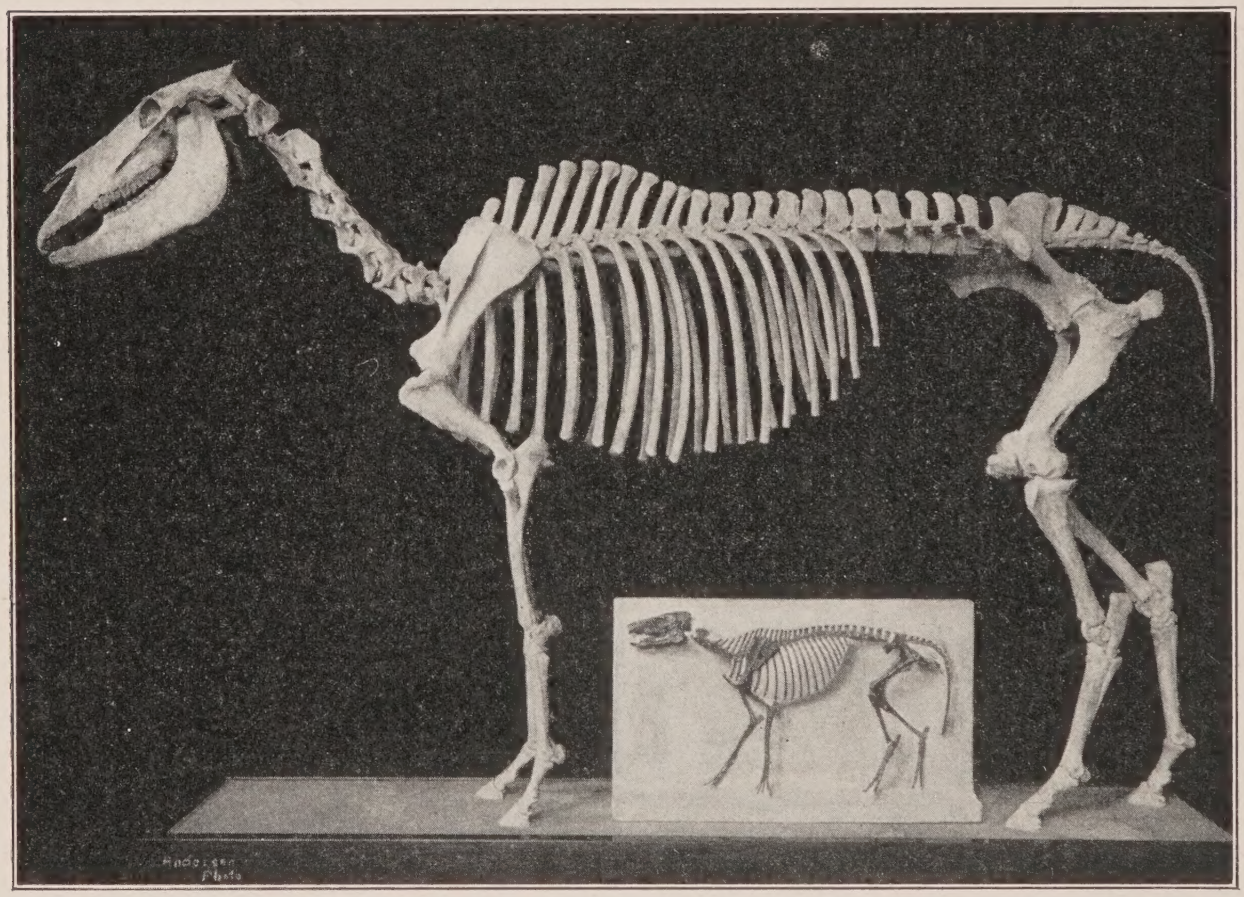


FIG. 14. — Duration of the Age of Mammals as measured by the evolution of the horse. Skeleton of the Eocene four-toed horse, *Eohippus*, and of the Texas Lower Pleistocene horse, *Equus scotti*. In the American Museum of Natural History.

the close of the Oligocene did the mighty system of the Swiss Alps begin to rise. Central Asia was even yet a plain and upland, and only during the Miocene did the Himalayas, the noblest existing mountain chain, begin to rise to their present fellowship with the sky. In North America again, since the close of the Eocene the region of the present Grand Cañon of the Colorado has been elevated 11,000 feet and the river has carved its mighty cañon through the rock to its present maximum depth of 6500 feet.

Those who have been impressed with a sense of the antiquity of these wonders of the world and will imagine the vast changes in the history of continental geography and continental life which were involved, will be ready to concede that the Age of Mammals alone represents an almost inconceivable period of time.

Modes of Estimating Cœnozoic Time

From the rocks themselves there are several modes of calculation: 1. *Total thickness* of the formations composing the so-called sedimentary rocks, compared with the average rate of accumulation, deposition, and sedimentation observable to-day. 2. *Denudation and erosion*, the counter processes, or the wearing away of elevated surfaces by the action of water and wind, snow, ice, and frost. Estimates of former heights of mountains, etc., and of the length of time during which these erosive agencies have been at work. 3. *Chemical content* of the sea, based on the assumption that all the salts and mineral elements of the sea are derived by solution from the soil. 4. *Procession and recession* of the glaciers as a means of estimating Pleistocene or Quaternary time by comparison of past with present advances and retreats of glacial masses.

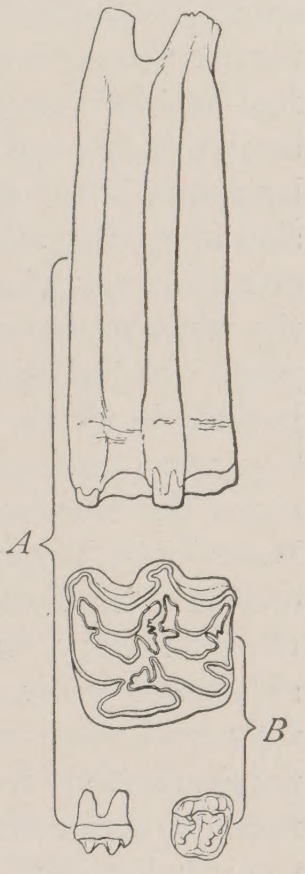


Fig. 15. — Duration of the Age of Mammals as measured by the evolution of the teeth of the horse. Superior grinding teeth of *Eohippus* (below), and of *Equus* (above), drawn to scale and showing the great increase in complexity as well as in length (*A*) and width (*B*).

Obstacles confront every mode of making these comparisons of past and present processes. In estimating past rates of *accumulation* by those observed in the deltas or mouths of existing rivers, the disturbing and unnatural influence of man must be considered. The modern delta accumulations of the Mississippi, the Po, the Danube, the Tigris, the Euphrates, and the Ganges are probably unnaturally rapid because the soil of the drainage basins from which these deltas are formed has been disturbed by the unnatural erosion hastened by human cultivation. In the case of the Tigris and Euphrates, the making of from forty to fifty miles of new land in the Persian Gulf, so that ancient seaports of four or five thousand years ago are now far inland, is very largely due indirectly to human agency, namely, to the destruction of the forests, the unrestricted browsing of sheep and goats, and the consequent rapid denudation of the soil.

Deposition or accumulation. — An outline of the methods employed to calculate rates of deposition may be found in Williams's "Geological Biology" (1895). The Mississippi, according to the calculations of Humphreys and Abbot, brings down every year sediment equivalent in amount to a mass 268 feet deep and one square mile in extent. Assuming the area of distribution to be 50,000 square miles, the deposit would reach a depth of 50 feet in about 10,000 years, or one foot in 200 years. Forshay estimated the Mississippi accumulation as four times as rapid, or at the rate of one foot in 50 years. The most precisely measured flood plain in the world is that on either

side of the River Nile. It is found that by the annual overflow the sediments accumulate at the rate of two feet and ten inches in 100 years.[1] Again, illustrating the difficulty of forming estimates from present rates of accumulation or deposition, the estimates given by Geikie in 1892 may be cited, which show that the sedimentary deposits at the mouth of the Po are much more rapid than those at the mouth of the Danube.

Denudation or erosion. — Estimates based on denudation confront similar difficulties. Haughton [2] in 1878 found the mean rate of denudation of the surface in the several great river basins of the world to be one foot in 3090 years. A most ingenious method of measuring the rate of erosion is the 'cedar-root chronology,' which appears to have been invented by James Hall [3] in 1871. He made an elaborate study of the rate of erosion along the valley of the Mohawk River in New York, based upon the estimated age of nineteen cedar trees, the length of the exposed root, and the recession of the cliff per century. From this he calculated that 35,000 years was the minimum of time since the Cohoes Falls were opposite the pothole in which the famous 'Cohoes mastodon' skeleton was deposited. The same method was used by Knight [4] in 1899, of especial interest because the observations were made in a well-known fossiliferous area, at Bates-Hole, Wyoming, where there is a vast depression produced by the erosion of the Tertiary beds of Oligocene Age. On its slopes grow pine trees (*Pinus murrayana* Eng.) that have recorded the rate of erosion here for about 300 years. As the material was worn away their roots became more and more exposed. The oldest of the trees stand on slopes, their trunks elevated three or four feet above the slopes. On the average it was found that the trees 300 years old had about three feet of rock removed from their roots. According to this 100 years are required to remove one foot of surface. Three miles have been eroded on either side, and at the rate of one foot per century, 1,584,000 years must have elapsed since the process began. The process began not earlier than the close of the Miocene, when the highest beds of Bates-Hole were deposited. Thus the erosion must have occurred during the subsequent Pliocene and Pleistocene periods, which estimated in this way represent a duration of 1,584,000 years. On this basis it would not be out of the way to estimate the Age of Mammals at 4,000,000.

Helium content. — The most recent method is that of Strutt, based upon the amount of helium found in different rocks. Helium, like the radioactive elements, accumulates in minerals, and hence if we measure

[1] Lyons, H. G., The Physiography of the River Nile and its Basin. Surv. Dep't. Egypt, Cairo, 1906.

[2] Haughton, Physical Geology. *Nature*, Vol. 18, 1878, pp. 266–268.

[3] Hall, J., Notes and Observations on the Cohoes Mastodon. *Rept. N. Y. State Cab. Nat. Hist.*, Vol. 21, 1871, pp. 99–148.

[4] Knight, W. C., Some New Data for Converting Geological Time into Years. *Science*, n.s. Vol. X, 1899, pp. 607–608.

the amount of helium in a sample rock and the amount produced in the sample in one year, we can reckon the length of time the helium has been accumulating, and hence the age of the rock. This method may lead to determinations not merely of the average age of the crust of the rock, but of the ages of particular rocks and the date at which the various strata were deposited.[1]

A very rough estimate of the accumulation or thickness of the Eocene and Oligocene sediments in the Rocky Mountain basins is seven thousand feet. This is an approximate figure which will in time be made exact. These sediments, however, consist largely of tuffs or partly worked over volcanic materials deposited in water. We certainly have no means of comparison with similar processes going on to-day which will enable us to estimate the time occupied in the accumulation of these rocks.

Thus difficulties confront us on every side, and the most careful of our computations are mere approximations. Since, however, it is desirable to give some idea of the scientific opinion on the duration of the Age of Mammals, the following table is of interest.

LENGTH OF CÆNOZOIC ERA OR AGE OF MAMMALS

Estimated by Comparison with Present Rates of Deposition and Denudation

Dana	1874	3,000,000 years	Based on the estimated thickness of the total series of stratified rocks and the estimated rate of *accumulation* of deposits along the shores of continents at the present time.
Wallace	1881	4,200,000 years (Tertiary = 4,000,000 Quaternary = 200,000 +)	Based on the rate of *denudation* with the estimated thickness of sedimentary rocks (which is probably less than 177,200 feet, as given by Haughton '78); and further on the dates of phases of high eccentricity of the earth's orbit.
Walcott	1893	2,900,000 years	Based on the total thickness of sedimentary rocks of North America (100,000 feet), compared with present rates of *accumulation*.
Upham	1893	3,100,000 years (mean) (Tertiary = 2 − 4,000,000 Quaternary = 100,000)	Based on estimates of the length of the glacial stages.

[1] Thomson, J. J., Address of the President of the British Association for the Advancement of Science [Winnipeg, 1909]. *Science*, n.s. Vol. XXX, no. 765, Aug. 27, 1909, pp. 257–279.

Knight	1899	4,000,000 years (Eocene-Miocene = 2,500,000 app. Plio.-Pleistocene = 1,584,000)	Based on the rate of *denudation* or erosion as measured by the amount of exposure of roots of pine trees of known age (1 foot in 100 years).
Sollas	1900	4,200,000 years (Tertiary = 3,800,000 Quaternary = 400,000)	Based on the rate of *accumulation* estimated at 1 foot in 100 years. The estimated thickness of sedimentary rocks (Eocene to Recent) is 42,000 feet.
	1909	6,380,000 years	The thickness of sedimentary rocks (Eocene to Recent) estimated at 63,800 feet.
Penck	1908	Quaternary = 500,000 to 1,000,000 years	Based on the average rate of *denudation* of the present land surface ($\frac{1}{3600}$ foot in 1 year).

VI. The World Supply of Mammals

The source of the world's supply of mammals, the great homes, centers, or continents from which the orders evolved and took on their distinctive

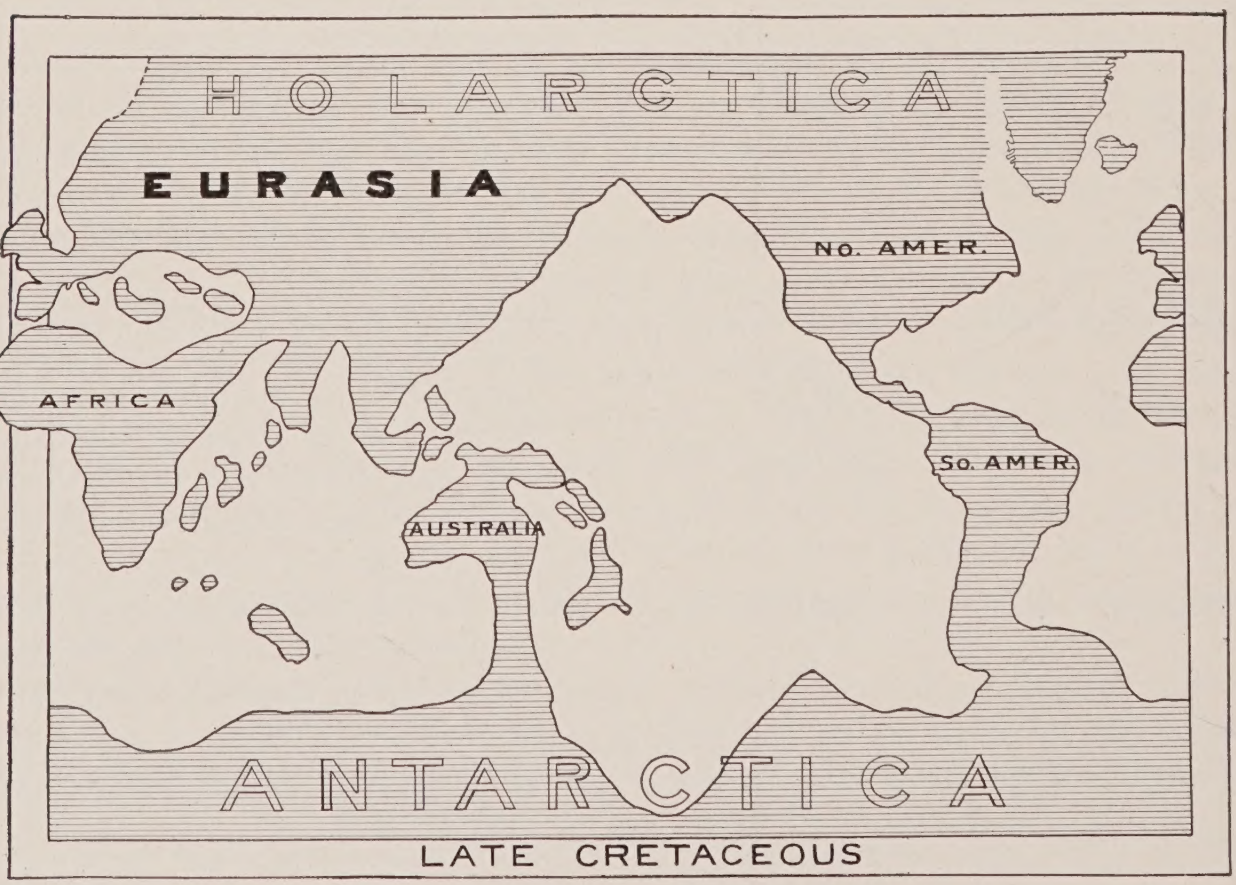


Fig. 16. — **Late Cretaceous and Basal Eocene.** Period of extinction of the great Reptilia. A time of elevation, favoring an interchange of archaic life between South and North America, also between North America and Europe. South America probably united with Australia via Antarctica, allowing an interchange of carnivorous and herbivorous marsupials. A partial community of fauna between North America and Eurasia with Africa. Rearranged from W. D. Matthew, 1908.

form, still remains as one of the great problems of the Age of Mammals which has not been thoroughly worked out. The solution turns upon palæogeography, or the past relations of the continents and islands to each other, but many palæogeographic problems in turn appeal to the past and present distribution of animals and plants. The existence of a great southern continent, Antarctica, for example, is just beginning to be demonstrated through geography and geology;[1] it was first indicated through the facts of palæontology, zoölogy, and botany.

Thus we may first briefly consider the distribution of mammalian orders in the past, and then the *palæogeography*, or former distribution of land surfaces, migrating tracts, etc.

World-wide distribution during the Age of Reptiles. — Our comparison begins with Eocene times, or the first period of the Age of Mammals. We find proofs from the very outset not only that all the great continents were richly supplied with mammalian life, but that during the preceding Age of Reptiles important migrations and interchanges of mammalian life had taken place, establishing a sort of cosmopolitan distribution of the more primitive forms, especially of the Insectivora. These generalized stem forms of mammals were widely distributed. We discover (compare p. 64) during the latter part of the Age of Reptiles and very early in the Age of Mammals evidences of connections between the following areas:

Australia, deriving its marsupials either from the north through Asia and the northern continents, or from the south through Antarctica and South America.

South America, sharing a community of marsupial life with Australia either through Antarctica on the south or through North America, Europe, and Asia on the north, and of placental life with (?) North America.

North America, sharing a community of life in the orders Marsupialia, Edentata, and probably Condylarthra and (?) Amblypoda on the south with South America, and on the north with Europe and probably Asia.

Africa, showing evidence of a community of mammalian life with Europe on the north and Asia on the northeast, but as yet no evidence of connection either with the mammalian life of Australia or the early mammalian life of South America.

Mammals of the Northern Hemisphere. Holarctica the Grand Center of Evolution

As regards the grand centers of origin, Rütimeyer in his classic paper of 1867 set forth what is now known as the *Bi-polar* theory.[2] Other authors have advocated the *North Polar* theory; others again the *South Polar* theory (Ameghino).

[1] The recent British Antarctic expeditions confirm the pioneer geographic work of Wilkes, and report the discovery of sedimentary deposits and of fossilized wood.

[2] Rütimeyer, Ueber die Herkunft unserer Thierwelt. Basel und Genf, 1867.

The North Polar Theory. — Since the greater land masses of the globe are in the north, we should expect to find a greater number of orders of mammals in the northern hemisphere than in the southern (see p. 68). In 1886 Haacke advanced the extreme theory that all land mammals originated at the North Pole and thence spread southward.[1] To support this theory it was only necessary to assume land connections between the north polar region and the northern parts of Europe, Asia, and North America, connections between North and South America, between Europe and Africa, between Africa and Madagascar, between Asia and Australia, and between Australia and New Zealand. The climate of the North Pole, according to this theory, was subtropical. In migrating to the south new forms pressed the old ones until the older were forced down to the southern extremities. This would account for the ancient orders of Monotremata and Marsupialia in Australia and for the Marsupialia in southern portions of North America and in South America. The fact that the present continents have as a whole had the same geographic boundaries for long periods of time supports Haacke's theory, which does not presuppose any essential changes in the masses of water and land and renders unnecessary the hypothesis of a southern creative center, such as Antarctica. We shall see, however, that there are many facts which can be explained only through the existence of such a great southern land mass.

Similarly in 1903 Wortman,[2] calling attention to the proofs of a mild and equable climate growing very gradually cooler as characteristic of the north polar region throughout the early part of the Age of Mammals, assumed the existence of a grand northern common center of evolution and dispersal, both for plants and animals. Such a general southward retreat of the higher plants and mammals throughout much of the Age of Reptiles and the whole of the Age of Mammals appears to be demonstrated by a succession of waves of migration, utterly unheralded, certainly not coming from the south (that is, from either South America or Africa) and thus as certainly coming from the north, *i.e.*, from a northerly formative evolution area. These southward waves are partly to be ascribed to the lowering of temperature which was inaugurated at the Pole and gradually extended southward.

Scharff [3] also has favored this theory of a northern creative center of mammalian life. He believes in North Atlantic land connections which must have existed up to very recent geological times between northern Scandinavia and Arctic North America by way of Spitzbergen and Greenland; in fact, in early Pliocene times or perhaps during the Miocene Period

[1] Wilh. Haacke, Der Nordpol als Schöpfungscentrum der Landfauna. *Biolog. Centralblatt*, Vol. 6, 1886–1887, pp. 363–370.

[2] Wortman, Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum, Pt. II, Primates. *Amer. Jour. Sci.*, June, 1903, Vol. 15, pp. 419–436.

[3] Scharff, R., European Animals: Their Geological History and Geographical Distribution, New York, 1907.

an extensive continent united northern Europe and Arctic North America. The southern shores of this continent extended from the British Isles to Newfoundland in a great curve. He points out that the fossil flora proves that the subsidences of the northern Atlantic which separated Europe and America were geologically recent, that is, of late Pliocene and Pleistocene times. So few remains of fossil mammals have been found on the eastern coast of North America that the hypothesis of Scharff of a broad North

FIG. 17. — Chief centers of the adaptive radiation of the orders of mammals so far as known at the present time.

Atlantic land connection during a considerable part of the Age of Mammals is neither supported nor disproved by such negative evidence.

Other authors [1] believe that the connections and migration routes between Europe and North America were chiefly North Pacific or via Asia and the region of Behring Straits.

Even if the north polar center theory of Haacke be extreme and the evidence for a north Atlantic land mass is less strong than that for North Pacific land connection between the New and Old worlds, the fact remains undisputed somewhat in the form stated by Wortman, that the northern portions of Europe, Asia, and North America formed the greatest creative center, probably during the Age of Reptiles and certainly during the Age of Mammals. Striking evidence for this is found in the great number and variety of the orders of mammals which have been discovered early in Eocene and Lower Oligocene times in Europe and North America, which with Asia constitute the region Holarctica.

These orders of mammals (compare p. 73) are as follows:

[1] See Matthew, W. D., Hypothetical Outlines of the Continents in Tertiary Times. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXII, Art. XXI, Oct. 25, 1906.

Marsupialia	Pholidota
Insectivora	Tubulidentata
Chiroptera	Lemuroidea
Carnivora-Creodonta	Condylarthra
Carvornia-Fissipedia	Amblypoda
Rodentia	Artiodactyla
Tillodontia	Perissodactyla
Tæniodonta or Ganodonta	Ancylopoda
Edentata-Xenarthra	Zeuglodontia

This imposing array may, it is true, be partially swollen by inclusion of orders of mammals which were probably indigenous to South America (Edentata) and possibly to Africa (Pholidota, Tubulidentata, Zeuglodontia), but even taking out these possibly or probably foreign members of northern society, a large residuum of mammals which probably originated in the northern hemisphere still remains and firmly establishes this as the dominant hemisphere in the evolution of the Mammalia.

Africa, Ethiopian Region, also an Important Center of Mammalian Evolution

Regarding Africa as a theater of mammalian evolution there have been two views. First, the older view that Africa derived its original primitive stock of mammals from the north and then remained passive until it received a new wave of highly specialized mammals. Second, the newer view that Africa was throughout the Age of Mammals a great center of mammalian evolution and contributed its full quota to the world stock of modernized mammals. In general it may be said that prior to 1900 the African continent as a great theater of adaptive radiation of the Mammalia had not been sufficiently considered. This was chiefly because it had practically no discovered fossil mammal history. It was the fashion with most writers on geographic distribution to speak mainly and exclusively of the invasion of Africa by European types rather than of the possible invasion of Europe by African types.

Hypothesis of northern invasion of Africa.—In 1867 Rütimeyer[1] expressed the opinion that at a very early period Europe sent into Africa its wealth of tropical forms. The ancient population of this continent was first fully discussed by Alfred Russel Wallace,[2] who also set forth the hypothesis of northern invasion, namely: that before Pliocene times Africa was occupied only by a small primitive fauna, lemurs, insectivores, edentates, and rodents, and that early in Pliocene times the large mammalian fauna of Europe and southern Asia (Pikermi and Siwalik Hills) were "poured into Africa and, finding there a new and favorable country almost wholly unoccupied by large mammalia, increased to an enormous extent, developed into new forms, and finally overran the whole continent."

[1] Rütimeyer, Über die Herkunft unserer Thierwelt, 1867, pp. 42–43.

[2] Wallace, The Geographical Distribution of Animals, 1876, p. 288.

In his notable paper of 1876 Blanford [1] clearly implied the existence of an African element in the fauna of India, but he referred to mammals rather of recent than of early evolution in Africa. He believed [2] that an Indo-African land connection (the LEMURIA of other authors) across the Indian Ocean, persisted through the Age of Reptiles and probably lasted into early Cænozoic times, vestiges of this connection being indicated by Madagascar, the Seychelles, and other islands and coral reefs. Madagascar continued to form a part of the African mainland throughout the first half of the Age of Mammals, but was severed from it before Africa was *invaded from the north,* in older Pliocene and glacial times. Madagascar possesses among its fauna (Insectivora, Lemuroidea) the older mammals of the African continent which have become little modified since. Blanford also believed [2] (1890, p. 73) in a connection between Africa and South America, in order to explain certain supposed alliances between some South American and African and even Madagascan types.

Similarly Lydekker [3] (1896) believed that the ancestral types of the existing mammals of Madagascar entered the African continent some time during the Oligocene period and soon after ranged over the whole of the Ethiopian and Malagasy (Madagascar, Mascarene Islands) regions, which were then broadly united and possessed a common mammalian fauna. In Lydekker's opinion, Africa was peopled only with these primitive forms and not until the Pliocene Age, when Madagascar became isolated as an island, did there occur the great invasion from the north of the higher and larger mammals such as apes, monkeys, and the great quadrupeds which were then flourishing all along southern Europe and Asia. This migration took place (p. 256) along the eastern side of the continent and the existence of certain species of mammals which are still common to India and Africa, or were so during the Pleistocene epoch, lends support to this view.

Similar theories were expressed in 1888 by Schlosser,[4] namely, that the mammals of Africa seem to be partly (1) a continuation of the primitive animal life found in the North American Eocene, and partly (2) a continuation of the European and Asiatic life of the Upper Eocene. Thus the present mammalian fauna of Africa seems to point to *two migrations:* (1) the first occurred very early, including the primitive Insectivora, closely related to forms found early in the Age of Mammals in North America; (2) the second migration into Africa occurred in the Pliocene, bringing in the apes, cats, hyænas, civet cats, rhinoceroses, horses, elephants, pigs, hippopotami, antelopes, etc. Up to this time these mammals had lived in Europe or in Asia.

[1] Blanford, W. T., The African Element in the Fauna of India. *Ann. Mag. Nat. Hist.*, Ser. 4, Vol. XVIII, 1876, pp. 277–294.

[2] *Id.*, Address Delivered at the Anniversary Meeting of the Geological Society of London, Feb. 21, 1890, p. 68 (*Proc. Geol. Soc.*, 1890, pp. 43–110).

[3] Lydekker, A Geographical History of Mammals, Cambridge, 1896, p. 255.

[4] Schlosser, M., Über die Beziehungen der ausgestorbenen Säugethierfaunen und ihr Verhältniss zur Säugethierfauna der Gegenwart. *Biol. Centralbl.*, 1888, Vol. VIII, pp. 582–650.

Hypothesis of Africa as an evolution center. — The opposing view of the invasion of Europe from Africa was independently thought out and set forth by three authors in 1899–1900, namely, by Tullberg in his monograph on the rodents,[1] by Stehlin in his monograph on the teeth of the pig family,[2] and by Osborn.[3]

Tullberg, as directly opposed to Haacke, is a strong believer in a great southerly center of distribution, and stands, like Rütimeyer, as an advocate of the bipolar theory. Thus he remarks (pp. 490–491):

"In the Miocene the great African region sent its heterogeneous fauna into Asia by way of Syria or Arabia. In this way Eurasia received together with typical (southwest) African types, others of Asiatic origin that had become differentiated from their ancestral forms, in the Madagascar-East-African region. Among the latter may be counted the Cavicornia, which, though a product of Africa, were most likely originally derived from northern Artiodactyla. The Simiæ, Proboscidea, and the rodent Hystricognathi are probably purely African types whose first appearance in Eurasia followed the Miocene migration." When the Placentalia first appear they have already undergone a considerable differentiation, and since they sprang neither from the Marsupialia nor from the Monotremata, we must assume that they went through the early undiscovered stages of their evolution in some great geographic region (other than Australia); this region is presumably the great southerly continent embracing South America and Africa and reaching over to India by way of Madagascar with a broad tongue of land (the Lemuria and Gondwana Land of other authors). Three great mammalian groups had already evolved: (1) the ancestors of the Lemuroidea and Anthropoidea; (2) the ancestors of the Ungulata; (3) the ancestors of the Rodentia-Simplicidentata. These stocks segregated off into two great divisions: one, East-Africa-Madagascar-Europe-Asia-North-America, the other Southwest-Africa-South-America. In the beginning of the Age of Mammals, Africa became separated from South America; in the Lower Oligocene (p. 488) Madagascar separated both from Asia (India) and from Africa. At the same time, however, the east African region joined with the southwest African region and an interchange of mammals took place.

Stehlin's views (p. 478) are still more closely parallel to those independently developed by Osborn, as the following citation from his monograph [2] shows:

"Africa's part in the evolution of the animal life of the globe (p. 478) has generally been represented as very passive, but the mere fact that Africa was a large continental landmass during the entire Tertiary makes this view seem untenable. Among the living mammals of Africa there are a number of types such as the coney (*Hyrax*), the aardvark (*Orycteropus*), and the pangolin (*Manis*), which differ so widely from any Tertiary Asiatic or European forms, that the conclusion

[1] Tullberg, T., Über das System der Nagethiere, 1899, pp. 485–495.

[2] Stehlin, H. G., Über die Geschichte des Suiden-Gebisses, 1899–1900, pp. 478–488.

[3] Osborn, H. F., Faunal Relations of Europe and America during the Tertiary Period and Theory of the Successive Invasions of an African Fauna into Europe, 1900, pp. 56–59.

seems not far to seek that they represent the last remnants of an ancient African fauna. This hypothetical (p. 479) primitive fauna was clearly analogous to that of South America, and it seems probable that there existed a means of communication between the two continents either by way of Antarctica or a trans-Atlantic landmass. It is possible that both had received their fauna from the north in pretertiary times. Certain it is, however, that both were later connected with the northern continents, communication in the eastern hemisphere being established much earlier than in the western, probably before the Miocene. Africa is now inhabited by mammalian types of various orders, which have become differentiated into genera and even families, and which are practically unknown among the fossil as well as the living fauna of Europe and Asia. When we consider how large a space of time is required for the development of even slight modifications, *the conclusion seems forced upon us that a large proportion of the present faunal types of Africa existed there throughout the Tertiary.* The antelopes (p. 480), then as now, seem to have had their chief centre of evolution in Africa, and perhaps the giraffes likewise. Whether the horses, rhinoceroses and even the enigmatical proboscideans were native to the same continent in early Tertiary times, must remain an open question. It is *very probable* (p. 488) *that the Pikermi fauna* [a rich Upper Miocene fauna of Greece, see map, p. 267], save for the forms that can be referred back to the European middle Miocene, *is derived from Africa.* The way into Asia seems to have been less open at this time, no African forms having been found east of Maragha (Persia). In the Pliocene, on the other hand, communication with Asia seems to have been more intimate than with Europe. It is a remarkable fact (p. 488) that *Chœropsis* (the pigmy hippopotamus), and *Phacochœrus* (the wart-hog) at no time migrated out of Africa. Perhaps Ethiopia was better able to maintain its inhabitants uninterruptedly than any part of Asia or Europe because it remained for the most part unaffected by the great marine and orogenic movements, and by the great lowering of temperature at the close of the Tertiary."

In 1899–1900 Osborn developed and published his "Theory of Successive Invasions of an African Fauna into Europe." He observes (p. 56):

"Let us therefore clearly set forth the hypothesis of *the Ethiopian region or South Africa as a great center of independent evolution* and as the source of successive northward migrations of animals, some of which ultimately reached even the extremity of South America — I refer to the Mastodons. . . .

"The *first* of these migrations we may suppose brought in certain highly specialized ruminants of the Upper Eocene, the anomalures or peculiar flying rodents of Africa; with this invasion may have come the pangolins [Pholidota] and aardvarks [Tubulidentata], and possibly certain armadillos, *Dasypodidæ*, if M. Filhol's identification of *Necrodasypus* is correct. A *second* invasion of great distinctness may be that which marks the beginning of the Miocene when the mastodons and dinotheres first appear in Europe, also the earliest of the antelopes. A *third* invasion may be represented in the base of the Pliocene by the increasing number of antelopes, the great giraffes of the Ægean plateau, and in the upper Pliocene by the hippopotami. With these forms came the rhinoceroses with no incisor or cutting teeth, similar to the smaller African rhinoceros, *D. bicornis.* Another recently discovered African immigrant upon the Island of Samos in the Ægean plateau is *Pliohyrax*

or *Leptodon*, a very large member of the Hyracoidea, probably aquatic in its habits, indicating that this order enjoyed an extensive adaptive radiation in Tertiary times."

"It thus appears that the Proboscidia, Hyracoidea, certain Edentata, the antelopes, the giraffes, the hippopotami, the most specialized ruminants, and among the rodents, the anomalures, dormice, and jerboas, among monkeys the baboons, may all have enjoyed their original adaptive radiation in Africa; that they survived after the glacial period, only in the Oriental or Indo-Malayan region, and that this accounts for the marked community of fauna between this region and the Ethiopian as observed by BLANFORD and ALLEN."

Osborn contended that against the prevalent theory of Asiatic origin of these mammals were two important facts: first, that the known Oligocene and Lower Miocene mammals of the Bugti beds of Sind are markedly European in type, and contain no African elements; second, that if these animals had originated in Asia some of them would have found their way into North America as early as or earlier than into Europe; third, there is the important fact that all these animals appear suddenly in Europe without any known ancestors in the older geologic formations.

This hypothesis of Osborn up to the present time, however, appears to be confirmed only so far as the Proboscidea and Hyracoidea are concerned.

Autochthonous orders of Africa. — These hypotheses of Tullberg, Stehlin, and Osborn, that Africa has been an important center of adaptive radiation, enjoyed a partial but most welcome verification in 1901 when Mr. Hugh J. L. Beadnell of the Geological Survey of Egypt and Dr. C. W. Andrews of the British Museum of London announced the discovery of numerous fossil land mammals in Upper Eocene and Lower Oligocene strata exposed in the Fayûm about eighty miles southwest of Cairo. Between 1901 and 1905 the exploration and collection of these beds were actively continued.[1] One unexpected discovery succeeded another: Africa, far from being a continent parasitic upon Europe and Asia, was proved through these discoveries to be a partly dependent but chiefly independent center of a highly varied life, a great breeding place not only of animals which subsequently wandered into Europe, but of

[1] Andrews, A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. London, 1906.

Osborn, H. F., Milk Dentition of the Hyracoid *Saghatherium* from the Upper Eocene of Egypt. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXII, Art. xiii, July 25, 1906, pp. 263–266.

Osborn, H. F., The American Museum Expedition to the Fayûm Desert. *The Nation*, Vol. 84, no. 2177, Mar. 21, 1907, pp. 271–272.

Osborn, H. F., The Fayûm Expedition of the American Museum. *Science*, n.s. Vol. XXV, no. 639, Mar. 29, 1907, pp. 513–516.

Osborn, H. F., Hunting the Ancestral Elephant in the Fayûm Desert. Discoveries of the Recent African Expedition of the American Museum of Natural History. *The Century Magazine*, Vol. LXXIV, Oct., 1907, no. 6, pp. 815–835.

Osborn, H. F., New Fossil Mammals from the Fayûm Oligocene, Egypt. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, Art. xvi, Mar. 25, 1908, pp. 265–272.

Osborn, H. F., New Carnivorous Mammals from the Fayûm Oligocene, Egypt. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVI, Art. xxviii, Sept., 1909, pp. 415–424.

animals belonging to types hitherto unknown and undreamed of. The ancestors of the two great groups which Osborn had hypothetically placed on the map of Africa, namely, the Proboscidea and the Hyracoidea, were successively found here as well as the remarkable unknown group of Embrithopoda, including *Arsinoïtherium*. The Sirenia or seacows, which had been discovered many years earlier near Cairo, were traced back to primitive forms, and then the ancestors of the archaic whales, or Zeuglodontia, a group also previously discovered here, were traced back to their early stages of evolution. These discoveries proved to be epoch-making, marking a turning point in our knowledge of the origin and distribution of the Mammalia, and arousing such widespread interest that for the time being North Africa becomes the storm center of mammalian palæontology. (See p. 199.)

From our present knowledge it appears that Africa may have been, therefore, the *source* or original home of the following orders of mammals:

Proboscidea,	Mastodons and elephants.
Sirenia,	Seacows or manatees and dugongs.
Zeuglodontia,	Primitive or ancestral whales, showing evidence of descent from land-living, carnivorous forms.[1]
Hyracoidea,	Large ancestral forms of the modern diminutive 'dassies' and conies.
Embrithopoda,	Represented by the giant *Arsinoitherium*, a large herbivorous quadruped with a pair of great horns on the front part of the skull.

Autochthonous and migrant orders of Africa. — It is well to place in immediate contrast with the list of Holarctic Orders on p. 68 all those orders of mammals which have thus far been found in the Eocene and Oligocene of northern Africa in the Fayûm region, keeping in mind most emphatically that this probably represents only a part of the whole mammalian fauna of Africa in these early geological times, and that great discoveries are still to be made, especially among the order Insectivora. These mingled orders *present or discovered* in Africa are as follows:

Carnivora-Creodonta
Rodentia-Theridomyidæ
Artiodactyla
Proboscidea
Primates
Sirenia
Embrithopoda
Hyracoidea
Zeuglodontia

Certain orders of mammals are conspicuous by their *absence* from this ancient Ethiopian list, although one or more of them may well be found when we know more of the palæontology of the "dark continent." Among these *absent* or *undiscovered* forms are:

[1] Zeuglodonts are also observed in the Upper Eocene of the eastern United States.

Tillodontia	Amblypoda
Tæniodonta	Perissodactyla
Edentata	(an especially notable absence)
Pholidota	Ancylopoda
Tubulidentata	Carnivora-Fissipedia
Condylarthra	(also an especially notable absence)

In other words, this early African assemblage is conspicuously lacking in the perissodactyl or odd-toed ungulates (horses, tapirs, and rhinoceroses), so abundantly represented at the same time in the north, also in the characteristic pangolins (Pholidota) and aardvarks (Tubulidentata) which are now widely spread in Africa. The raptorial animals of early African times are solely of the archaic type of Carnivora known as Creodonta, and do not include representatives of the dog, cat, hyæna, or civet families. Even anticipating the modification and enlargement of this limited assemblage by future discovery, the conclusion is certainly supported by fact as at present known that Africa formed a very important independent center of adaptive radiation during the Eocene and early Oligocene period.

Early migration between Europe and Madagascar. — Still more recently (1905) Grandidier [1] has discussed the former zoögeographic relations between Europe and Madagascar, as shown in the following citations: [1]

"The lemurs, as well as many others of the existing and extinct mammals of Madagascar, show a close affinity to Eocene types of France. *Cryptoprocta ferox*, the curious plantigrade cat known as the 'Fossa,' is allied to *Proailurus* and *Pseudælurus*. The viverrines are allied to *Cynodictis*. The Madagascan hippopotamus is perhaps allied to *Acotherulum*. Of birds, *Æpyornis*, so abundant among the extinct animals of Madagascar, is comparable to *Dasyornis londinensis* of the Eocene of the Isle of Sheppey, England. It seems thus that the last representatives of the Eocene fauna of the north took refuge in Madagascar. This faunal community is explicable only on the assumption of intermigrations between Europe and Madagascar, perhaps by way of Africa, in the early Tertiaries. If 'Lemuria,' the great Indo-Madagascan continent, of which Madagascar is supposed to be the sole remnant, ever existed, it must have been reduced to a long Indian peninsula or archipelago in Mesozoic times. It is much more logical to suppose that during the Tertiary the northwest coast of Madagascar for a short time became united with the mainland of Africa by an isthmus, of which Mayotte, the Comores, etc., are remnants. By means of this land bridge Madagascar was peopled not only with African animals such as *Hippopotamus* and *Potamochœrus*, but also with the Eocene and Oligocene types so widely distributed in the northern hemisphere, and remains of which appear also in Egypt, India, etc. Communication with Africa was finally interrupted and Madagascar continued its independent existence, its inhabitants evolving without admixture of strange elements and maintaining their primitive characteristics. Meanwhile Africa received ruminants, large Carnivora, etc., by immigration, forms which are totally lacking in Madagascar."

[1] Grandidier, G., Recherches sur les Lémuriens Disparus et en particulier sur ceux qui vivaient à Madagascar. *Extr. Nouv. Arch. Mus.*, Ser. 4, Vol. VII, Paris, 1905. (See especially pp. 138–140.)

Antarctica, Australia and South America

One of the greatest triumphs of recent biological investigation is the hypothetical reconstruction of a great southern continent, to which the name Antarctica has been given, through the concurrence of evidence derived from botany, zoölogy, and palæontology. This tends to support the bipolar theory.

In 1847 the British botanist Sir Joseph Hooker first advocated the view that there had been a larger and more continuous tract of land than now exists in the Antarctic Ocean, to explain the distribution of flowering plants, which show the same resemblances as the animals, many plants of Chili, Patagonia, Tasmania, and New Zealand being allied. He did not assign any geological date whatever to his Antarctic land. In 1867 the Swiss palæontologist Rütimeyer published his remarkable zoögeographical sketch entitled *Uber die Herkunft unserer Thierwelt.*[1]

He says (pp. 13–15):

"From the study of modern distribution and particularly of island life, we arrive at the conclusion that all parts of the earth, no matter how isolated, have received their animal inhabitants from a few faunal centers. Aside from the large connected land masses north of the equator, we need to assume only three such centers for the warm-blooded animals of both hemispheres: Australia for the marsupials, Madagascar for the makis, and the islands of the Indian Ocean from New Zealand to Madagascar for the wingless birds. In reality these three centers are one, since their fauna represents *the remnants of the animal life of a large Antarctic continent,* since covered by the sea and by an impenetrable ice-sheet. The presence of marsupials and of ostriches in America and of penguins on both sides of the great body of water that divides the continents from the South Polar regions, are evidence in favor of such an assumption." Besides this *Antarctic* faunal center Rütimeyer also believed in an Arctic or northern faunal center (p. 65).

In 1870 Huxley,[2] in his anniversary address before the Geological Society of London, said that the simplest and most rational way of accounting for the various differences and similitudes of the life of southern lands is on the supposition that a South Pacific continent existed during the Age of Reptiles which connected Australia, New Zealand, and South America, and then gradually subsided, Australia being the first land to be cut off from the connection and thus receiving only the lower types of mammals, or marsupials. This took the form of a supposed South Atlantic rather than South Pacific land bridge. In 1893 H. O. Forbes[3] revived Hooker's theory of a southern or Antarctic continent, and considered that it existed until very late times geologically, that is, until the Pliocene. He even proposed to connect this

[1] For full reference see Bibliography.

[2] Huxley, Anniversary Address of the President, 1870. Collected Memoirs, Vol. III, p. 548.

[3] Forbes, H. O., The Chatham Islands; their Relation to a Former Southern Continent. *Roy. Geog. Soc.*, Suppl., Vol. III, 1893; and, Antarctica, a Supposed Former Southern Continent. *Nat. Sci.*, Vol. III, 1893.

continent with Madagascar and with some of the Polynesian Islands of the South Pacific. In 1895 Charles Hedley,[1] an Australian naturalist, proposed the more reasonable view of the extension of the Antarctic continent, supposing that in mid-Tertiary time, during the period of milder climate, a continent somewhat larger than that now existing at the Antarctic Pole connected South America with Tasmania and with New Zealand. From this continent he supposed that the marsupials, reptiles, amphibians, and snails, which are common to South America, Australia, and New Zealand, may have migrated.

The history of this fascinating Antarctica theory is fully narrated by that expert palæogeographer Arnold Edward Ortmann.[2] It was discussed by Gill (1875) in its relation to the distribution of the fishes. Evidence in its favor has been drawn by Beddard from a study of worms and other invertebrates: by Moore from a study of the flora of South Africa; by Spencer from a study of the Australian fauna; by Ameghino, Hatcher, and Ortmann from observations on the invertebrate and vertebrate fossils of Patagonia; by Moreno from the discovery in South America of *Miolania*, an Australian fossil turtle.

In 1900 Osborn[3] reconstructed this old continent by elevation to the 3040 meter sounding line, as shown in the accompanying figure, thus presenting a view intermediate between the extreme of Forbes and the more conservative view of Hedley, who had united South America with Tasmania through a narrow strip of land. Ortmann, in 1901, after reviewing the whole subject,[4] accepted the first theory of Rütimeyer with the restrictions put upon it by Hedley, expressing the opinion that the fossil shells and mammals of Patagonia resemble certain forms of New Zealand and Australia so closely as to be regarded as an additional proof of the former connection of South America with Australia and New Zealand, *but not with Africa*. This author also reconstructed Antarctica.

Later opinions on the subject are those of W. J. Sinclair (1905) based on his exhaustive studies of the marsupials of Australia and Patagonia,[5] from which he concludes:[6] "The Patagonian marsupials of the Santa Cruz epoch are of peculiar interest from the relationship which they bear to certain Australian and Tasmanian forms. This relationship establishes the reality of former land connection between the Australian region and South

[1] Hedley, C., Considerations on the Surviving Refugees in Austral Lands of Ancient Antarctic Life. *Proc. Roy. Soc. N.S. Wales*, 1895; and, A Zoögeographic Scheme for the Mid-Pacific. *Proc. Linn. Soc. N.S. Wales*, 1899.

[2] Ortmann, Reports of the Princeton Expedition to Patagonia, Vol. IV, Palæontology I, Pt. 1, Marine Cretaceous Invertebrates, 1901, p. 310.

[3] Osborn, Faunal Relations of Europe and America, 1900, p. 52.

[4] Ortmann, The Theories of the Origin of the Antarctic Faunas and Floras. *Amer. Natural.*, Vol. XXXV, no. 410, Feb., 1901, pp. 139–142.

[5] Published in the Princeton Patagonian Reports, Vol. IV, Pt. 3, 1906, pp. 330–460.

[6] Sinclair, The Marsupial Fauna of the Santa Cruz Beds. *Proc. Amer. Philos. Soc.*, Vol. XLIX, no. 179, 1905, pp. 73 ff.

America, so plainly indicated by the distribution of the Tertiary marine mollusks, fishes, land shells, decapod crustacea, and plants."

Equally emphatic is the conclusion of Dollo based on the fishes collected by the Belgian Antarctic expedition.[1] After citing (pp. 220–222) the whole

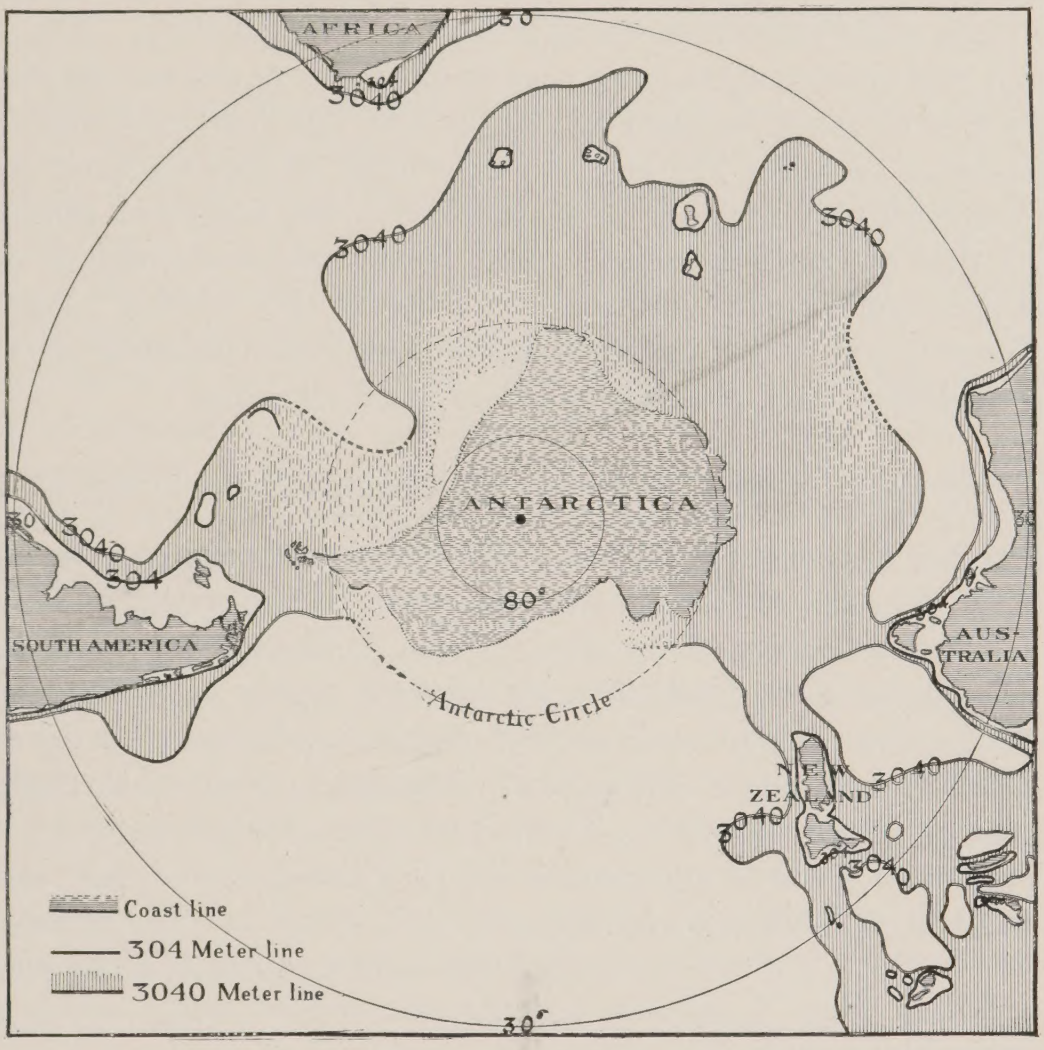


FIG. 18. — South polar view of the world, elevated to the 3040 meter line, showing the actual (horizontal lines) and the hypothetical (vertical lines) outlines of the continent Antarctica, including its supposed relations with New Zealand and Australia. After Osborn.

history of the discussion of the existence of a South Polar continent, he considers the distribution of five families and four genera of freshwater fishes, and concludes (p. 224) that in the present state of our knowledge it is the Tertiary Antarctica of Osborn or an analogous Antarctica, indispensable for the marsupials and the turtle, *Miolania*, which best explains the biogeography of the Antarctic and sub-Antarctic fishes.

Australasia or Notogæa

The highly specialized mammals, monotremes and marsupials, of Australasia are so remote geographically and zoölogically from the history of the northern hemisphere that it is only necessary to state two principal facts.

[1] Dollo, Résultats du Voyage du S. Y. Belgica en 1897–1898–1899, Zoologie, Poissons. 4to. Anvers, 1904.

First, the anatomy of these mammals points back to the introduction into Australia of some small arboreal opossum or *Didelphys*-like forms as the source of the wonderful adaptive radiation of the marsupials of this continent. Whence this *Didelphys*-like form came, whether from Asia or from Antarctica, is unknown, and why the placental insectivorous forms did not enter the continent at the same time is also a mystery. The present imperfect palæontological evidence favors the entry of marsupials into Australia by way of South America and Antarctica, but it must be remembered that this turns upon the fact that our knowledge of pre-Oligocene mammal life of Asia is entirely a blank. The affinities of the Australian mammalian life with that of South America consist in the common presence of both the polyprotodont or carnivorous forms, allied to the existing "Tasmanian wolf" (*Thylacinus*), and of the small diprotodont herbivorous forms (epanorthids, *Cœnolestes*), very remotely allied to the kangaroos.

South America or Neogœa, A Theater of Evolution Equal to that of Africa

South America appears to have had late Cretaceous or early Eocene connections through Antarctica with Australia on the south, and with the great northern radiation of mammals of the northern hemisphere through North America. This constituted its original supply of mammalian life, from which sprang a grand and peculiar adaptive radiation after the connections both with Australia and with North America were cut off through either geographic or climatic barriers. There is no satisfactory evidence of connection at any time with the mammalian life of Africa except in very late Pliocene times through migration by way of North America. The twelve orders of mammals which evolved in South America from these original sources of supply include three (primates, rodents, and odontocetes) which apparently arrived later than the remainder.

Mammalian Orders of Pre-Pliocene Times, South America

Marsupialia	Condylarthra (identification doubtful)
Insectivora (rare)	Toxodontia
Rodentia of the suborder Hystricomorpha only	Astrapotheria
Edentata	Litopterna
Anthropoidea [1] (Platyrhini)	Pyrotheria
	Cetacea (Odontoceti)

Conspicuous by their *absence* from the pre-Pliocene formations of South America are the following orders:

Chiroptera	Artiodactyla
Tillodontia	Perissodactyla

[1] It is important to note that the South American monkeys are widely distinct from the Old World or catarrhine monkeys and apes.

Tæniodonta	Ancylopoda
Pholidota	Sirenia
Tubulidentata	Embrithopoda
Lemuroidea	Hyracoidea
Amblypoda (possibly represented)	Zeuglodontia
	Proboscidea

We can most readily understand the absence of the four peculiarly African orders, the Proboscidea, Sirenia, Hyracoidea, Embrithopoda. The peripty-chid family of Amblypoda is possibly represented by some animals described by Ameghino. The absence of many orders highly characteristic of the Eocene of the northern hemisphere is more striking, namely, Artiodactyla, Perissodactyla, Ancylopoda, Chiroptera, Carnivora-Fissipedia. The mammalian history of South America during the Age of Mammals is further remarkable because of the extinction of the Insectivora which are apparently represented in the small Lower Miocene genus *Necrolestes*, which is analogous to the *Chrysochloris* or Cape golden mole of South Africa.

An interesting parallel with Africa in Eocene and Oligocene times is in the entire absence of true Carnivora of the dog or cat families, whose function of preying upon the Herbivora and other mammals was exclusively performed in Africa by the archaic Creodonta, and in South America by the archaic carnivorous Marsupialia. This freedom from attacks of the higher specialized carnivores constituted a condition especially favorable to the wonderful adaptive radiation in South America of the opossums (Didelphyidæ), hystricomorph rodents (cavies, tree porcupines, viscachas), as well as edentates (sloths, armadillos, glyptodonts, anteaters), and of four very specialized and peculiar orders of ungulate type.

General Conclusions

This review of the sources of the world's supply of mammals shows that there were various degrees of kinship or community of life between the continents, as follows: (1) close kinship of the Holarctic Region, namely, North America, Asia, and Europe, having the majority of the pre-Miocene orders of mammals in common, and separated chiefly by the apparently early contributions of Africa to Europe and of South America to North America; (2) separation of the Africa-Ethiopian Region as a center of evolution of four or five orders of mammals not found elsewhere, although united with Europe by the presence in common of two orders of mammals and probably others to be discovered; (3) South America, with the closest early kinship with North America, more ancient kinship with Australia, remote kinship with Europe, and still more remote kinship with Africa. These degrees of relationship are just what we should expect from a bird's-eye view of the geography of the northern and southern hemispheres respectively.

VII. Palæogeography

The present and past geographic distribution of the mammals, their migrations, their sudden invasions, afford most valuable data for the science of *palæogeography*. Through this science we attempt to restore the former outlines of the continents and seas. While, as shown by Wallace, small mammals may be carried over sea considerable distances on driftwood, and while many of the larger mammals are capable of swimming great distances, it is certain that the distribution and colonization of the large terrestrial mammals have only taken place through land connections between the various continents and islands. We are, in fact, forced again and again to assume the existence of such land connections, but this fact does not enable us to plot the former geographic outlines. To do this we require evidence furnished by geology, which with the aid of that furnished by fossil shells makes it possible to trace the former invasions of the sea over what is now land, and even to establish closely certain ancient shorelines. The conclusions drawn from existing and fossil mammals must also be compared with those drawn from the distribution of birds, reptiles, fresh and sea water fishes, insects, and other invertebrates, and in a very important degree of plants.

Palæogeography is still an embryonic or nascent science with great possibilities of future growth and usefulness. The hypothetical outlines of the continents during the Age of Mammals as presented in this volume are reproductions with slight modifications of those published by Matthew.[1] These outlines represent a synthesis of the work of De Lapparent, Dall, Hill, Hatcher, and others.

They are to be interpreted, as originally stated by their author, as both hypothetical and temporary. The author himself has now (1910) abandoned as a matter of imperfect record the theory of an Antarctic land connection between South America and Australia, as represented in his map of the world in post-Cretaceous time, on p. 64 of this volume. He now believes that the greater part of the animals and plants of the southern continents are of northern origin, and that the evidence advanced for Antarctic connections is probably explainable through distribution from the north.

Asiatic-American land bridge. — The theory of a North Pacific land bridge over what is now Behring Straits still depends largely on the evidence afforded by the distribution of the mammals, because the Cænozoic geology of Alaska and of northeast Siberia is so imperfectly known. The most interesting fact concerning this land bridge is that both from zoölogical and palæontological data it appears to have been intermittent, to have emerged from the sea and then to have become submerged. American geologists have concluded that the northwestern coasts of Alaska and British Columbia were above water during the Eocene to an extent as great or greater than at present.

[1] Hypothetical Outlines of the Continents in Tertiary Times. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXII, Art. xxi, 1906.

Submergence of the coast during Oligocene and Lower Miocene times was succeeded by a reëmergence, known as the post-Kenai revolution, in late Miocene or Early Pliocene times. The mammalian life of Europe and North America similarly shows intermittent intervals of close correspondence and similarity and of separation or divergence. The very close similarity between the mammals living at the present time on either side of the Behring Straits is strong evidence that up to late Pleistocene times there was free migration between the two continents.

The Great Antilles, West Indies, and South America. — This region was another area of emergence and submergence, which is of deep interest because of the apparent faunal connection between North and South America late in the Age of Reptiles and early in the Age of Mammals, followed by a prolonged and absolute separation or divergence of the mammalian life of the two countries, which was again succeeded by a sudden renewal of relations in the Middle Pliocene. The results obtained by Hill (1899)[1] as to the movements of the Antilles are summarized by Matthew as follows: "The Eocene strata of the Antilles bear evidence of the preëxistence of extensive areas of land during the latter part of the Age of Reptiles (Cretaceous). Late in Eocene time there was a profound submergence including all but the highest tips of the Antilles, which lasted into early Oligocene times. In Oligocene or Miocene times there was a great upward movement whereby many of the islands were connected with each other and possibly with the insular southern portion of Florida, but land connections between the North and South American continents were not established at this time. During Miocene and Pliocene times the islands were again separated by partial submergence into their present outlines, which have been since retained with only slight modifications. In Pliocene and Pleistocene times there have been intermittent periods of elevation, but none so great as those in the latter part of the Oligocene."

These conclusions on the whole leave the question of the period of connection between North and South America entirely an open one; yet this period seems to be pretty firmly established as of Pliocene Age through the overwhelming testimony of the interchange of large terrestrial mammals between North and South America at this time.

[1] Hill, R. T., Geological Reconnoissance of Jamaica. *Bull. Mus. Comp. Zoöl.*, Vol. XXXIV, 1899, pp. 1–226.

CHAPTER II

THE EOCENE OF EUROPE AND NORTH AMERICA

The Eocene was originally defined as the dawn of the recent species of marine molluscs. It subsequently came to be regarded also as the dawn of mammalian life. We now realize that it was more truly the sudden expansion and evolution of the mammals after what appears to have been a long

Fig. 19. — Chief areas in which mammal deposits of the Age of Reptiles have been discovered. **1**. North America, Laramie (Cretaceous), Judith River (Cretaceous), Morrison (Jurassic); **2**. North Carolina (Upper Triassic); **3**. Germany (Upper Triassic); **4**. England, Purbeck (Upper Jurassic), Stonesfield slate (Middle Jurassic); **5**. South Africa, Stormberg Beds (Upper Triassic). **6**. Patagonia (Age doubtful).

period of very slow development during the Age of Reptiles. The true dawn of the mammals had occurred some 15,000,000 years earlier, even before the opening of the Age of Reptiles. This is truly a blank historic period, somewhat in the sense in which the term is applied to human history, because during the Age of Reptiles our documents are very rare and widely scattered. The few black dots on the accompanying map of the world are placed on all the geographic points on the entire globe where the remains of mammals of the Reptilian Age have thus far been recorded.

Even these dots may give an exaggerated idea of our knowledge, because the remains which have been discovered consist largely of teeth and imperfect jaws. The conditions which so favored the preservation of the records of reptilian life were singularly unfavorable to the recording of mammalian life. Exactly the reverse conditions, namely, of extensive terrestrial and freshwater formations, prevailed during the Age of Mammals, so that the mammalian records are far more complete than those of the reptiles, amphibians, or fishes.

Palæogeography of Eocene Europe

During a considerable part of the Eocene epoch Europe was a small, isolated land area, peninsular and sometimes insular. Seas are known to have extended over the region of the Pyrenees, over Switzerland, southward over a large part of Africa, and eastward to China. In these seas the shells of Foraminifera, called nummulites, accumulated as 'nummulitic' limestones to the extent of 10,000 feet, especially in the areas which now represent the summits of the Alps and Apennines.

Despite the broad areas of depression which correspond with the present mountain ranges of the Pyrenees and Alps, the continent of Europe was beginning to assume its present outlines and conformation. To the north France was broadly united with Great Britain. The interior of France was mostly above water. Throughout the Eocene period there were two areas of continental depression and elevation. The first, along the northeast coast bordering Belgium; the second, along the southwest coast bordering the Gulf of Gascogne, in the region of the Pyrenees. It is chiefly in these areas that the great life zones were preserved. The succession of stages which successively record the geographic and life changes in the country now known as France are as follows:

Upper Eocene	(6) *Ludian*	In the Basal Eocene, or *Thanetian*, France was indented by great northern and southern gulfs. Along the former were the mammaliferous deposits of Cernay and La Fère. In the Lower Eocene, or *Sparnacian*, there was a great northern gulf bordered by lagoons. In the *Ypresian* France was separated from Spain. In the Middle Eocene or *Lutetian*, France and western Europe formed a great island separated by a broad channel from Eurasia and Asia.
Middle Eocene	(5) *Bartonian*	
	(4) *Lutetian*	
Lower Eocene	(3) *Ypresian*	
	(2) *Sparnacian*	
Basal Eocene	(1) *Thanetian*	

These disturbed conditions of the shorelines and of the regions which now constitute the great river basins of France explain the great variety of deposits in which the remains of fossil mammals are found, namely, the succession of marine, fluvio-marine, littoral, estuarine, lagoon, and swamp deposits throughout the entire Eocene period in France and England. Con-

ditions of deposition in western North America were entirely different; here we find continuous depositions of uniform character. In France there is a lack of stability, due to weak or unstable coast outlines, to the alternation of land and sea deposits. Moreover, the relations of these land masses to each other and to the Asiatic continent were continually changing. The proximity of the sea favored a warm, moist, and uniform climate.

Palæogeography of North America

The most important thing to note, as pointed out by Suess, is that North America has been a relatively stable continent since the close of the Cretaceous; its great land surfaces are older, more prominent, and more extensive than those of Europe. The land surfaces of Africa, however, are far older than either.

It is the West which best repays interest, and the most central fact established is that there were during the Cænozoic Period two grand natural divisions of geologic deposition and of animal and plant habitat, similar to the two natural divisions which exist to-day, namely, the Mountain and the Plains regions. The Atlantic Border region becomes of importance only in late Cænozoic times. The Pacific Coast region becomes of importance in Pliocene and Pleistocene times.

For the purposes of our study, the palæogeography of the United States previous to the Pleistocene may therefore be divided into the following great regions:

1. The Atlantic Border Region.
2. The Plains Region.
3. The Mountain Region.
4. The Pacific Coast Region.

1. *Atlantic border region.* — More unstable conditions, somewhat similar to those of western Europe, may have prevailed along the eastern and Atlantic seaboard in Eocene times; that is, the north and south Atlantic borders were rising and falling. Only toward the end of the Eocene were portions of Florida raised out of the sea. The continental shoreline appears to have bordered the Atlantic in a general northeast to southwest direction from the region of southern New York to northern Florida. There was a well-marked indentation in southeast Georgia: from the vicinity of the Chattahoochee River the shorelines rounded to the west, northwest, and north, forming the eastern coast of a greater Gulf of Mexico which extended to the meeting of the Ohio and Mississippi Rivers. From this the Gulf extended in a southwesterly direction. At the culmination of the Eocene a movement of elevation took place. During the entire Eocene epoch the country stretching to the Mississippi and eastward to the Appalachians and Atlantic coast is, with a few exceptions, a *terra incognita* so far as its terrestrial mammalian life is concerned. Glimpses only of its marine or seashore mammalian life are afforded

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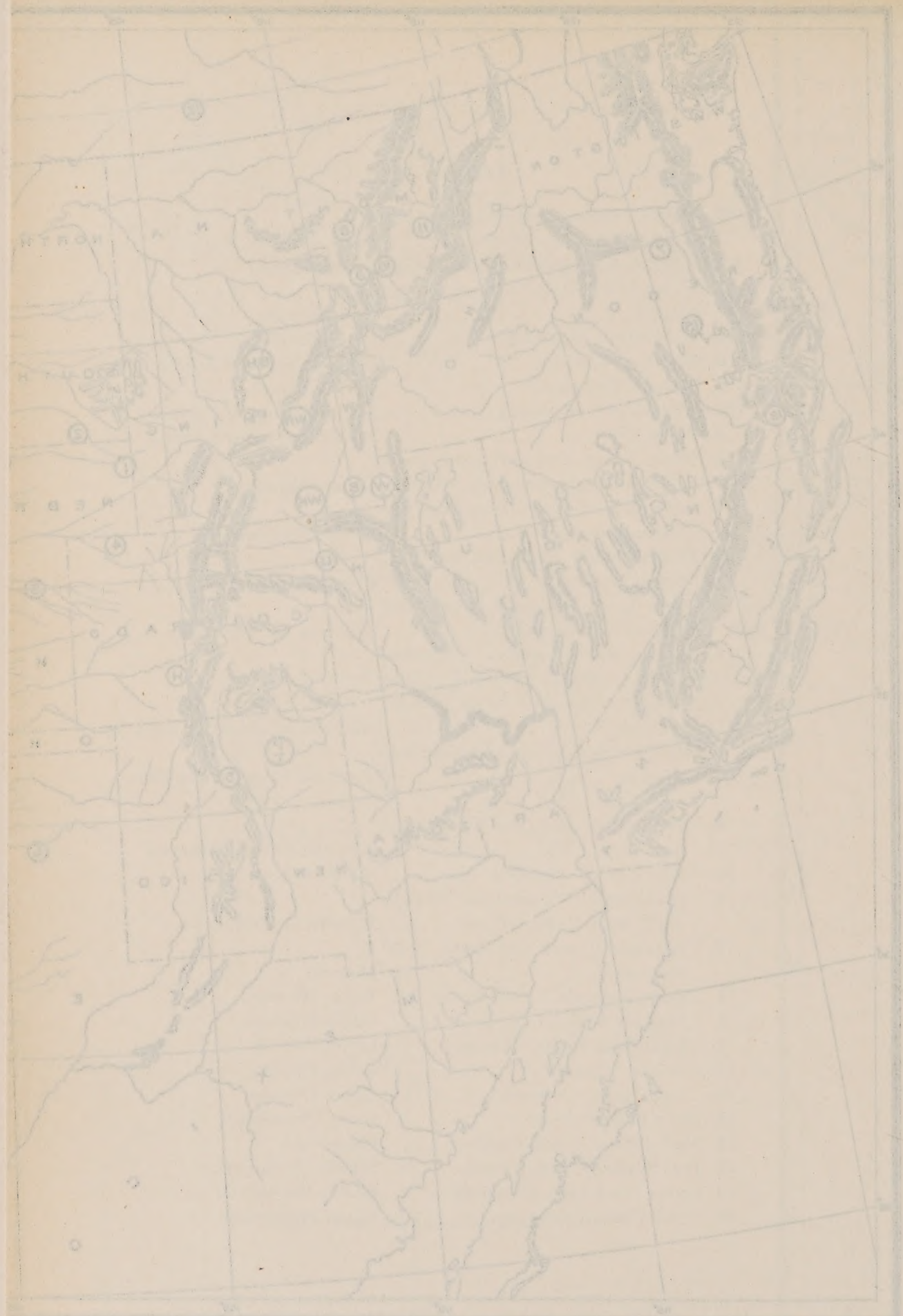
FIG. 20. — Map of the United States, showing the general Mountain and Great Plains Regions; also the typical localities of the principal formations, sections, and deposits.

KEY TO MAP

PT. Puerco, Torrejon, and Wasatch of San Juan basin, New Mexico ..... Basal and lower Eocene.
BH. Wasatch of Bighorn Basin, Wyoming. Lower Eocene.
W. Wasatch (typical), Evanston, Wyoming ..... Lower Eocene.
WR. Wind River, Wyoming ..... Lower Eocene.
H. Huerfano, Colorado ..... Lower and middle Eocene.
B. Bridger, Wyoming ..... Middle Eocene.
WK. "Washakie," Wyoming ..... Middle and upper Eocene.
U. Uinta, Utah ..... Middle and upper Eocene.
12. White River deposits along Swift Current Creek, Assiniboia, Canada . Lower Oligocene.
10. White River deposits along Pipestone Creek, Montana ..... Lower Oligocene.
2. Typical White River and Rosebud, South Dakota ..... Oligocene and Miocene.
1. White River, Monroe Creek, and Harrison, Nebraska ..... Oligocene and Miocene.
4. Pawnee Buttes section ("Pawnee Creek," "Martin Canyon," "Cedar Creek," "Horsetail Creek,") Colorado ..... Oligocene to middle Miocene.
7. John Day, Mascall, and Rattlesnake, Oregon ..... Oligocene, Miocene, and Pliocene.
8. "Fort Logan" and Deep River, Montana ..... Lower and middle Miocene.
11. "Flint Creek," Montana ..... Middle Miocene.
6. "Panhandle," "Clarendon," Blanco, and "Rock Creek," Texas ..... Miocene to Pleistocene.
17. "Nebraska," and underlying beds, Nebraska ..... Miocene.
5. "Santa Fe marls," New Mexico ..... Upper Miocene.
9. "Madison Valley," Montana ..... Upper Miocene.
3. "Republican River," Kansas ..... Lower Pliocene.
13. "Archer," Florida ..... Lower Pliocene.
14. "Loup River," Nebraska ..... Upper Pliocene.
18. Silver Lake, Oregon ..... Lower Pleistocene.
15. Ashley River, South Carolina ..... Pleistocene.
16. Port Kennedy, Pennsylvania ..... Middle Pleistocene.
19. Potter Creek cave, California ..... Middle Pleistocene.
20. Conard fissure, Arkansas ..... Upper Pleistocene.



in the Upper Eocene Zeuglodon Zone [1] (see p. 170) of Alabama and Florida, and in other littoral marine deposits.

While this vast eastern region contains no Eocene mammal-bearing deposits, it may well have been the scene of a very active continental mammalian life from the time of the emergence of the central area toward the close of the Cretaceous, or during and after Laramie time. Yet absolutely the only land mammals we know from this great region up to the Pleistocene are those reported by Marsh from the supposed Oligocene of New Jersey, namely, four species, the giant pig *Entelodon*, a tapiroid, *Protapirus* (*Tapiravus*) *validus*, a rhinoceros, *Rhinoceros matutinus*, and a supposed tillodont, *Anchippodus*. The animal last named is a Rocky Mountain Middle Eocene type, not known to have survived into Oligocene times.

2. *The plains region.* — The description of this region will be deferred until the introduction of the Oligocene (p. 204), with which epoch our records of plains life open.

3. *Mountain region.* — The mountain region contains the entire known record of Eocene continental life. The mountain and high plateau region as a whole stretched nearly through British Columbia to a broad land connection with Asia, which was apparently interrupted and renewed more than once during the Cænozoic. On the south it terminated in the mountains which form the northern boundary of the southern Mexican State Oaxaca. Of the great western mountain systems of the present time the Sierra Nevada range was formed at the close of the Jurassic Period, as announced by Whitney in 1864 and confirmed by Hyatt. Only toward the close of the Cretaceous (Laramie) did the present Rocky Mountain region begin to be defined by an uplift, commencing in Colorado and extending northward into Montana, accompanied by great volcanic outbursts, the Denver stage of Colorado, the Livingston stage of Montana, 7,000 feet in thickness on top of the Laramie. This mountain birth, extending from Mexico on the south to British America on the far north, and including a number of lesser ranges, gave rise to two great geographic features, namely: the *mountain basins* within the mountain region, and the *great plains* east of the mountain region, bordered on the south by the gigantic Gulf of Mexico.

In picturing in the mind's eye the mountain region in Eocene times it is very important to note that the Rocky Mountain ranges were far from having attained their present height; the highest emerged peaks in Eocene times were believed by Dana to have been perhaps 4,000 to 5,000 feet above sea level, while the Sierra Nevada ranges at the same time were between 3,000 and 4,000 feet above sea level. The Great Basin lying between the Rockies and Sierras was probably at a height of 1,000 feet above the sea.

During the subsequent Cænozoic the average elevation of the Rocky Mountain region was tripled, the mountain peaks in general rising from

[1] *Zeuglodon* is an aberrant whale-like form which probably originated in the early Eocene of northern Africa.

13,000 to 14,000 feet, with corresponding elevation of the intermediate basins and with a continuous erosion of their summits. The mountain ranges which were involved in this grand movement and defined the basin areas which are of such extraordinary interest to the palæontologist, are as follows: The Wasatch Range, which now extends north and south for over 100 miles on the east side of the Great Salt Lake Basin. East of the south half of the Wasatch Range, stretching away for 150 miles, are the Uinta Mountains (now over 13,000 feet in height); at the angle of a junction between these ranges is a great outflow of igneous rock (trachyte). Eastward of Utah, the Elk Mountains, the San Juan, and the Front Range of Colorado, including the famous Spanish Peaks, were uplifted. To the west the Pacific coast ranges, in time of elevation, lagged far behind the Sierra Nevada and even behind the Rocky Mountain ranges, remaining at sea level long after the Rocky Mountain system was born.

Mountain basin deposits. — The oldest basin is the San Juan (Fig. 21, PT) in northwestern New Mexico, which includes the Basal Eocene, Puerco and Torrejon, and Lower Eocene depositions, all lying on top of the Laramie or Upper Cretaceous. As displayed in the accompanying map (Fig. 21) the grandest basin area (W) is the Wasatch, lying east of the Wasatch Range and north of the Uinta Range, with an original width of 300 miles and north and south extent of 500 miles. This deposition concludes with the Lower Eocene Wasatch deposits, scattered over an area 450 miles north and south and 250 miles east and west to a thickness of 1,500 to 2,500 feet. Superposed on these deposits are the Green River shales, also Lower Eocene, and above these the Bridger (B) formation.

Mode of origin. — The underlying Wasatch is of fluviatile and flood plain origin, while the Green River shales cover an area of more than 5,000 square miles, and represent a vast shallow lake. The Bridger is regarded as fluviatile and flood plain, as is also the succeeding Washakie (WK). In northern Wyoming, west of the Big Horn Mountains, is another basin (BH) filled with a flood plain deposition of Wasatch age, and in west central Wyoming is the Wind River Basin (WR) of Lower and Middle Eocene age. East of the Front Range in southern Colorado, close to the Spanish Peaks, is the Huerfano Basin (H) of Lower and Middle Eocene age; and directly south of the Uinta Mountains is the great Uinta Basin (U), extending east and west over 140 miles and containing depositions of Middle and Upper Eocene age. To the northwest, in Oregon, are the John Day Basin (7) of Oligocene age and the Deep River (8) of Middle Miocene age.

The successive periods of deposition in these mountain basins is determined through the abundant remains of fossil mammals and other vertebrates which they contain, and it is a remarkable fact, brought out through palæontology, that these depositions were partly contemporaneous, partly successive, so that they give us a wonderful panorama of the entire succession

of life from the beginning of the Eocene to the end of Oligocene times, as shown in the diagram (Fig. 10) on page 49.

FIG. 21.—Chief Fossil Mammal Deposits of Western North America. **PT.** Puerco and Torrejon, N. Mex. **BH.** Big Horn Basin, Wyo. **W.** Typical Wasatch, Evanston, Wyo., and Utah. **WR.** Wind River, Wyo. **H.** Huerfano, Col. **B.** Bridger, Wyo. **WK.** Washakie, Wyo. **U.** Uinta, Utah and Col. **12.** Swift Current Creek, Assiniboia. **10.** Pipestone Creek, Mont. **2.** Typical White River and Rosebud, S. Dak. **1.** White River, Monroe Creek and Harrison, Nebr. **4.** Horsetail Creek, Cedar Creek, Pawnee Creek and Martin Canyon, Col. **7.** John Day, Mascall and Rattlesnake, Oreg. **8.** Fort Logan and Deep River, Mont. **11.** Flint Creek, Mont. **6.** Panhandle, Clarendon, Blanco and Rock Creek, Tex. **17.** "Nebraska" and underlying beds, Nebr. **5.** Santa Fe marls, N. Mex. **9.** Madison Valley, Mont. **3.** Republican River, Kan. **14.** Snake Creek, Nebr. **18.** Silver Lake, Oreg.

It was believed formerly that each of these great mountain basins contained a lake and that the deposits consequently were lacustrine, but the 'lake theory' has gradually given way to the theory that these were princi-

pally flood plain depositions, delta, overflow, and swamp deposits with relatively limited areas of shallow lakes. According to this theory the principal true lakes of Eocene and Miocene times are the Green River and the Florissant. The famous Green River formation consists of impure limestones and thin fissile calcareous shales often as finely laminated as paper, between the leaves of which we discover in beautiful preservation the remains of plants, insects, and fishes, but none of mammals except in the form of footprints. Occasional layers of gypsum indicate periods of evaporation and salinity. In the Bridger beds the frequent occurrence of large selenite

General Comparison of some of the Mountain and Plains Formations [1]

	MOUNTAIN BASIN DEPOSITS *Geologic.* — Partly of erosion materials; largely of volcanic materials, partly eolian, partly deposited in water. *Faunistic.* — Extinct mammals, chiefly inhabiting a mountainous, hilly, forested, lake- and river-border, well-watered country.	GREAT PLAINS DEPOSITS *Geologic.* — Largely of water-erosion and wind-erosion materials; partly of volcanic materials. *Faunistic.* — Extinct mammals, chiefly of an open-plains country, traversed by broad, slow-moving rivers, savannah, partly forested, with shallow lakes and decreasing rain supply.	
Middle Pliocene	. . . . .	Blanco, Tex.	Second deposition (or Neocene) period of very widespread fluviatile, flood-plain, and eolian deposits, chiefly erosion and volcanic materials, on the Great Plains of Dakota, Nebraska, Colorado, and western Kansas. Limited and scattered deposits in the Rocky Mountain region.
Lower Pliocene	Rattlesnake, Oreg. . . .	Ogalalla, in part ("Republican River"), Nebr.	
Upper Miocene	. . . . .	Ogalalla ("Nebraska"), Nebr.	
Middle Miocene	Deep River, Mont.; Mascall, Oreg.	"Pawnee Creek," Colo.	
Lower Miocene and Upper Oligocene	"Fort Logan," Mont. . . John Day (upper part), Oreg.	Arikaree (Gering, Rosebud), Nebr., S. Dak.	
Upper Oligocene	John Day (middle and lower parts), Oreg.	White River, S. Dak. (upper part).	
Lower Oligocene	Deposits on Pipestone Creek, Mont.	White River (lower part), of the western plains of South Dakota, Nebraska, etc.	
Upper Eocene	Uinta, northern Utah . .	. . . . .	First deposition (or Eocene) period of lacustrine, river, and flood-plain deposits, largely of volcanic materials in the Rocky Mountain basins, chiefly in the ancient drainage basin of Colorado River. Plains deposits of this period eroded away, buried, or unknown.
Middle Eocene	"Washakie," Wyo. . . . Bridger, Wyo.		
Lower Eocene	Wind River, Wyo. . . . Wasatch, N. Mex. and Wyo.		
Basal Eocene	Torrejon, N. Mex. . . . Puerco, N. Mex. . . . . Fort Union, Mont. . . .		

crystals proves that the water was occasionally unduly saline through evaporation. The existence of swamps in the Bridger is indicated by stretches of

[1] From p. 22 of Osborn, Cenozoic Mammal Horizons of Western North America. *U.S. Geol. Surv. Bull.*, 361. Washington, 1909.

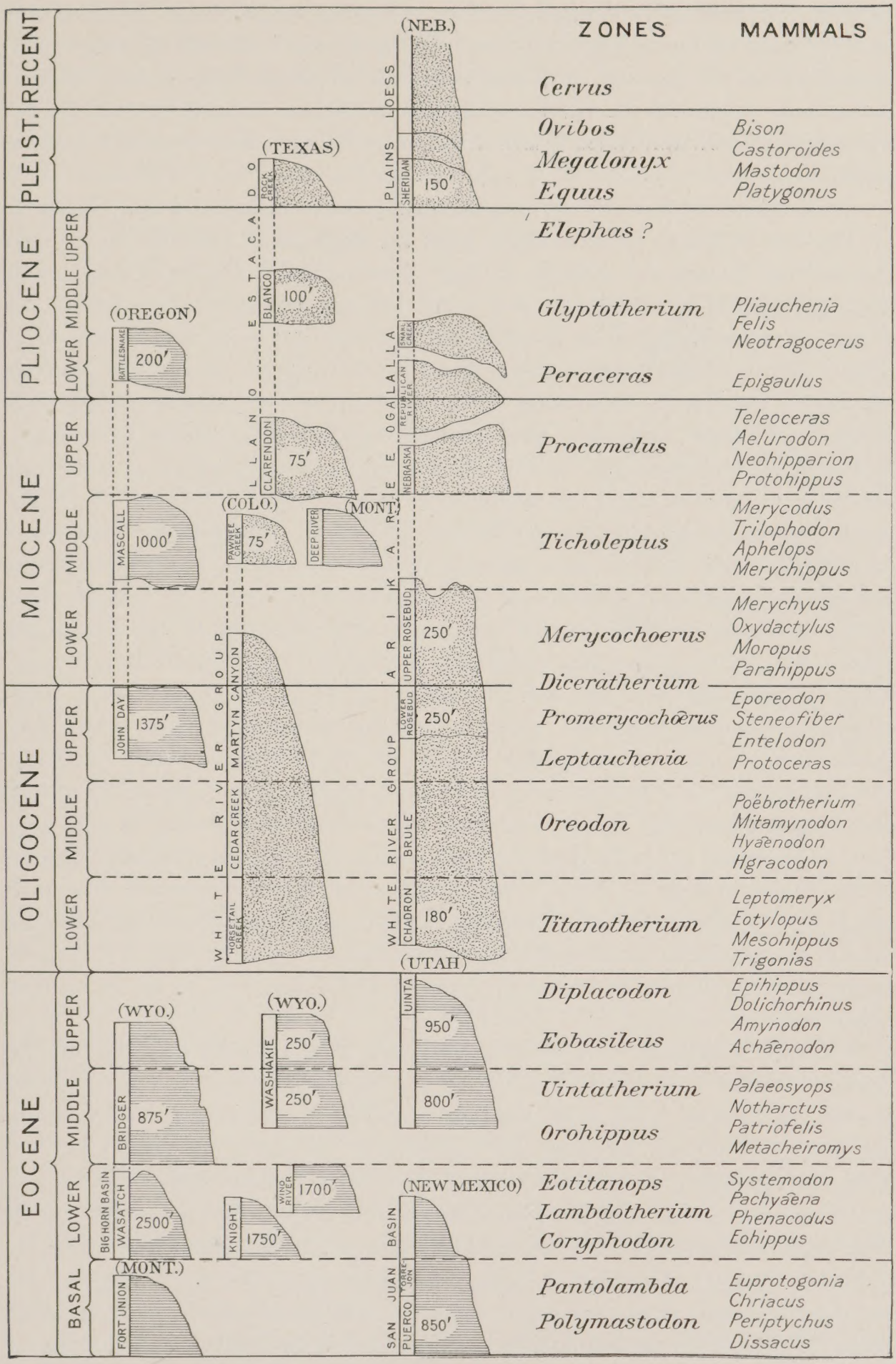


FIG. 22. — Composite of the more important sections, not drawn to scale, showing the principal Life Zones of the entire Cænozoic period in western North America. Mountain Basin deposits = horizontal ruling. Great Plains deposits = dotted areas.

lignite; the proofs of prolonged overflow or lagoon conditions are found in the great horizontal bands known as the "white layers." As will be more fully described below, the vast building materials of these deposits were partly derived by erosion from the surrounding mountain ranges, but chiefly by sediments of volcanic dust which have consolidated into what are known as tuffs.

These great facts of western physiography may be summed up as follows: (1) the axes of the mountain ranges were the same as at present; the ranges themselves, though not actually as high, were probably higher in relation to the surrounding country than at present because we must allow for a long period of erosion. (2) The Eocene drainage systems were also broadly the same as the modern, namely, the systems of the Colorado River, the Arkansas River, the Big Horn branch of the Missouri River, and the Columbia River. In details, however, the drainage systems have certainly been modified by uplift and erosion. (3) The deposits all lie in the same great mountain basins or mountain valleys in which they were originally collected. Owing to the proximity of volcanic peaks, ash and other fine eruptive materials contributed very largely and in some basins almost exclusively to these Eocene and Oligocene deposits of the Mountain region. (4) Except close to the mountain foothills, as, for example, in the Wasatch of the Big Horn basin (BH), there has been comparatively little post-Eocene disturbance, because these deposits are still horizontal or at gentle angles with their original horizontal position. (5) Surrounding mountain ranges were interspersed with active volcanic peaks; the upper Colorado River basin especially was surrounded by a circle of volcanoes which poured out their lava and widely distributed ashes. (6) The mammalian life of the mountain region is largely that of plateaux, uplands, and elevated basins, of streams and lake borders, of hillsides, and more or less of forests. There are also evidences of arid periods in which great stretches of the sandy flood plains were desiccated during the dry season of the year, and afforded a favorable basis for the evolution of mammals with slender or cursorial types of limbs and feet, as of the smaller horses.

Volcanic materials. — A very large part of the basin deposits of the Rocky Mountain Region which for years were described as consisting of gravels, sandstones, and clays, are now found to consist largely and in some places exclusively of volcanic ash materials. As early as 1876 Clarence King [1] recognized volcanic ash strata in the lower Eocene Wasatch of western Wyoming underlying the true Coryphodon Zone. Merrill and Peale in 1885–1886 determined the volcanic ash origin of the Bozeman Lake deposit, Gallatin County, Montana. Peale [2] prophetically observed: "Again, do not these volcanic materials which must have fallen in showers over a large extent of country — accumulating in some cases in beds 40 to 90 feet thick —

[1] King, C., *Amer. Jour. Sci.*, Ser. 3, Vol. XI, 1876, pp. 478–480.
[2] Peale, A. C., *Science*, Vol. VIII, Aug. 20, 1886, p. 163.

account for the perfect preservation of the vertebrate remains which characterize the formations in so many parts of the West: and is there not also suggested one possible cause for the extinction of some of the many groups of animals which have at present no descendants in this region and whose only remains are the bony fragments found in these lacustrine deposits?" Following Merriam's [1] determination (1901) of the volcanic ash nature of the

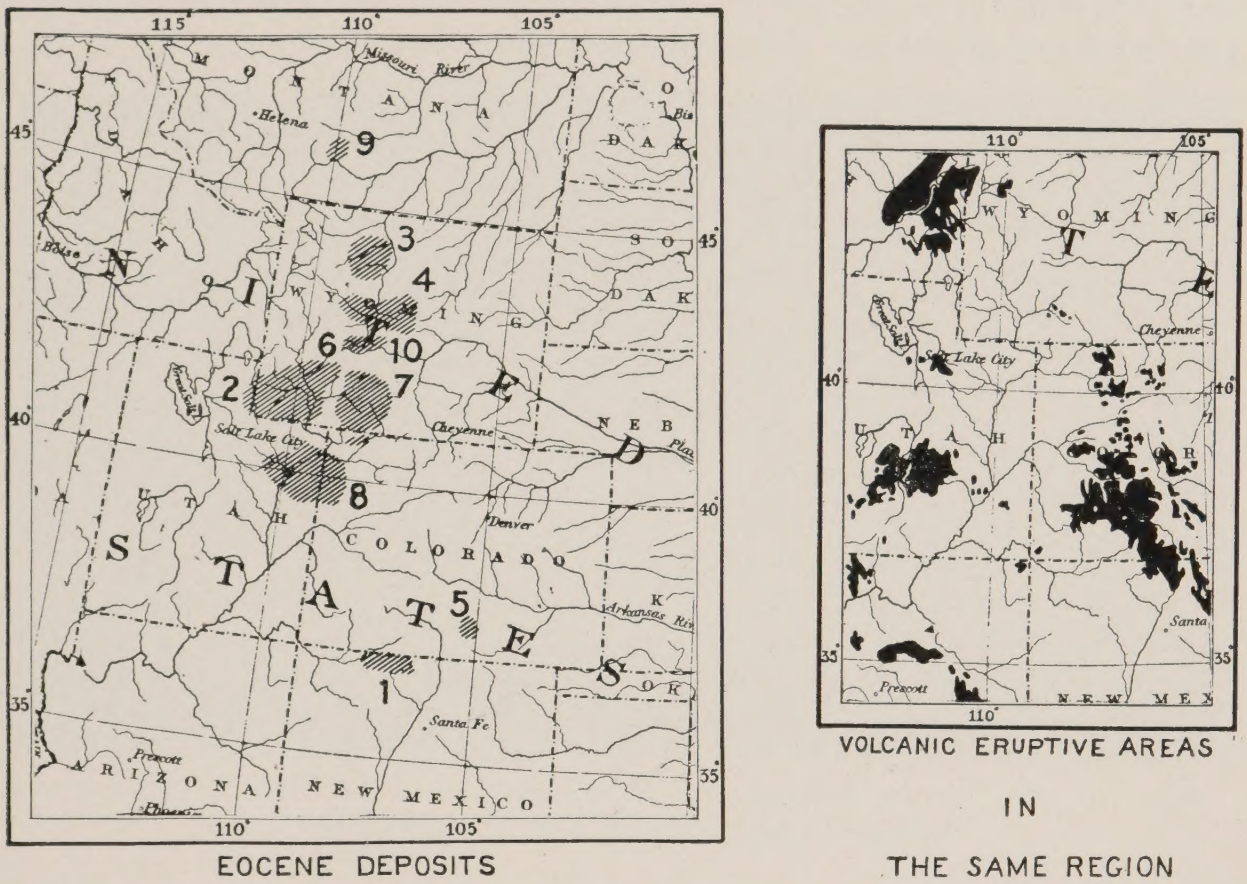


FIG. 23.—[To left] Chief Eocene fossil-mammal-bearing Formations (largely volcanic tuffs) in the Mountain Region of North America, and [to right] areas of volcanic rock (lavas) in the same geographic region. **1**. Puerco and Torrejon, N. Mex. **2**. Wasatch, Utah and Wyo. **3**. Big Horn (Wasatch), Wyo. **4**. Wind River, Wyo. **5**. Huerfano, Col. **6**. Bridger, Wyo. **7**. Washakie, Wyo. **8**. Uinta, Utah and Col. **9**. (?) Fort Union, Mont.

Oligocene deposits of the John Day Basin, the next important step was the recognition by Sinclair [2] (1906) that the deposits of the Bridger Basin (Middle Eocene) were also chiefly of volcanic nature, or tuffs. The same author [3] in 1907 proved that the successive Washakie Basin deposits were likewise of ash. This led to a thorough examination by the United States Geological Survey through Albert Johannsen of samples of rock from the entire Eocene Series, with the most interesting and conclusive results.[4]

The manner of deposition of the volcanic ash in these various basins,

[1] Merriam, J. C., A Contribution to the Geology of the John Day Basin. *Univ. Cal., Bull. Dept. Geol.*, Vol. II, 1901, p. 269.

[2] Sinclair, W. J., Volcanic Ash in the Bridger Beds of Wyoming. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXII, Art. xv, 1906, pp. 273–280.

[3] Sinclair, W. J., *Science*, n.s. Vol. XXVII, no. 685, Feb. 14, 1908, p. 254.

[4] Johannsen, Albert, *in litteris*, 1909.

whether washed down from the mountain sides, blown about on dry surfaces, distributed in flood plains or in extensive or shallow lakes, has not been fully determined. Merriam [1] rejects the theory of the lacustrine origin of the John Day Formation and speaks of "showers of ash with tuff deposits on a plain occupied in part by shallow lakes." Undoubtedly the wind or atmospheric currents were a great agent of distribution. As observed by Russell [2] one wind-distributed deposit in Alaska occupies 52,280 square miles, and is 100 feet thick in places. Other deposits cover great areas not only in the

FIG. 24. — Mt. Pelée and volcanic cloud distributing volcanic ash. After a painting by Charles R. Knight under the direction of E. O. Hovey.

mountain but in the plains region. As shown in the accompanying picture of Mt. Pelée, the dust is carried high up into the air by the explosive discharges of steam and gas, and may be distributed over vast areas by the wind. It is white unless adulterated with other substances, and resembles powdered pumice. It consists of angular flakes of glass, generally too small to be distinguished by the unaided eye. Its chief component is silica.

The total or combined thickness of these Eocene depositions is enormous, but since the deposits were partly contemporaneous and partly successive, as shown by a careful study of the life zones which they contain (diagram on p. 49), the net total Eocene deposition, deducting the thickness of overlapping deposits, was about 7,200 feet.

4. *Pacific coast, close of the Cretaceous.* — The subsidence and erosion of the western part of the western continent had almost established a connection between the Pacific gulf in California and Oregon and the old Mississippian Sea of the Mississippi valley.[3] The intervening isthmus not covered

[1] Merriam, J. C., *op. cit.*, 1901.

[2] Russell, I. C., Volcanoes of North America, New York, 1897, p. 286 fol.

[3] Smith, J. P., Salient Events in the Geologic History of California. *Science*, n.s., Vol. XXX, no. 767, 1909, pp. 346–351.

by salt water was worn down to base level, and widening expanses of flats were covered with marshes which eventually formed coal, preserving a similar flora from the outlyers of the Mississippi valley almost to the Pacific coast. These coal-forming conditions reached far up into Alaska, where almost under the arctic circle types of plants flourished that to-day could not live in the open, north of Mexico.

In Eocene times the climatic and geographic conditions remained the same, but the sea had encroached still farther on the land, and the base leveling of the backbone of the continent was more complete. Tropical conditions still prevailed up as far as Alaska, and coal was still formed abundantly where vegetation is now scanty. This is truly an "Eocene carboniferous," for most of the coal on the west coast belongs to this epoch. At this time also a temporary connection was established between the Pacific and Atlantic oceans, for the peculiarly Atlantic type of mollusc, *Venericardia planicosta*, is found along with Pacific types in California and Oregon.

In his recent discussion of this region, Scharff,[1] after a complete review of the existing knowledge of the present and former distribution of animal and plant life in the two continents, comes to the following somewhat extreme conclusion, namely: that there was a great lobe of land connecting western North America with the southern portion of the South American continent during the beginning of Cænozoic times, while Central America and the northern portion of the South American continent were still largely submerged.

Late Cretaceous and Early Eocene Flora

The plant life is naturally one of the keys to the evolution of the herbivorous mammals. We have to consider the food afforded by bark, leaves, twigs, and buds, by shrubs, and by the plants of softer tissue, such as mammals browse upon to-day, as well as by the grasses, plants of harder tissue, upon which they graze. The diminution of browsing mammals and increase of grazing mammals is one of the great features of Cænozoic evolution.

Grasses. — If we observe the conditions of the preservation of plant remains along existing ponds, river borders, or swamps we see at once that they are as favorable for the preservation of deciduous leaves as they are unfavorable for the preservation of grasses. Grasses are firmly attached to their roots and are not swept away either by water or wind. Leaf deposits, therefore, abound everywhere and give us sure indications of the forest flora, while we know but little of the field and meadow flora, which is of great importance in connection with the evolution of the grazing herbivorous Ungulates especially. In fact, the evidence as to grasses is very limited throughout the entire Age of Mammals. The number of kinds of grasses (Gramineæ) found in the whole Cænozoic of Europe is comparatively small, and it is diffi-

[1] Scharff, R. F., On an Early Tertiary Land-Connection between North and South America. *Amer. Natural.*, Vol. XLIII, Sept., 1909, pp. 513–531.

cult to draw conclusions from fossil plant remains alone as to their relative or absolute importance. At what period grasses began to assume anything like their present dominance it is impossible to determine. The absence of native grasses in Australia is indirect evidence of their late geological development. According to Schimper and Schenck [1] the first record of grasses is in the Cretaceous Age, the cane (*Arundo*), and the reed (*Phragmites*) being found in North America. According to Gardner [2] the determination of the meadow grass (*Poacites*) from the Komé beds of Greenland is very doubtful. There can be little doubt, according to Hollick, that grasses arose at an early period in the Cænozoic, perhaps even in the lowest Eocene. While Gardner (1886, p. 454) considers that they attained prominence in both hemispheres only toward the close of the Eocene, he believes it to be not improbable that they were established in the north (Spitzbergen) at an early period. The indirect evidence derived from the adaptations of the teeth of mammals disposes us to adopt the opinion of Gardner (1886, p. 441) that grasses attained wide distribution in both hemispheres only toward the close of the Eocene. Their evolution on favorable forestless regions was certainly a very prolonged one, beginning in Mesozoic times.

A southern flora. — The Tertiary flora in general [3] represents not only every one of the great types of vegetation but also a large number of the orders and genera of the present plant world. Passing over from the Cretaceous into the early Tertiary, the horsetails (Equisetaceæ) are represented by reduced forms. Among the gymnosperms, the cycads were waning while the Coniferæ, or true gymnosperms, were represented by forms closely allied to the sequoias, widely distributed and in great abundance. The true conifers or pines were of more modern origin. The palms were a dominant type which flourished in great luxuriance during the Eocene and Miocene. The dicotyledonous angiosperms which had appeared suddenly in the Upper Cretaceous began to gain complete ascendancy, and in this group were several types which seem to be waning at the present time: for example, the sassafras (*Sassafras*), tulip tree (*Liriodendron*), and the sweet gum (*Liquidambar*). In the Eocene a luxuriant vegetation covered the northern hemisphere as far north as Grinnell Land (81° 45′), the Arctic flora alone comprising 400 species of arborescent type. In North America the deciduous flora of the older Cænozoic was very similar to the modern flora.

The processes of modification and evolution of plants were far slower than the evolution of mammals. In connection with what has been said above regarding grasses, it is important to note that the deciduous plants which we know are mainly those which grow in the lowlands. In Cænozoic times, as now, there was a great difference in the vegetation of different

[1] Schimper und Schenk, Handbuch der Paläontologie (Zittel), II Abth., Paläophytologie, 1890, p. 385.

[2] Gardner, J. S., Fossil Grasses. *Proc. Geol. Assoc.*, Vol. IX, 1886, p. 441.

[3] Ward, L., Plants, Fossil, in Johnson's Universal Encyclopædia, 1895, p. 329.

levels. Temperature and humidity are the most important factors governing plant distribution, but we must also take into consideration the nature of the soil and other conditions of environment. Since there are so many factors governing plant distribution, it is difficult to use plants as thermometers of the past except in a general way, and this difficulty is increased by the fact that Cænozoic species are only related to and not identical with present species; also that many nearly related species can live under very different conditions.

The most memorable fact about the flora is one recently insisted upon by Knowlton (1909),[1] namely, that as we pass from the Cretaceous into the Eocene there is no appreciable change in the flora. From this it would appear that there was no secular change of climate; that the temperature remained the same. So impressed is this palæobotanist with these facts that he places within the Cretaceous the Fort Union Beds, which are here regarded as Basal Eocene.

ALTERNATE UNION AND DISUNION OF EUROPEAN AND NORTH AMERICAN LIFE

Europe and North America to-day are on the whole closely united in their mammalian life, and were it not for the profound changes and extinctions which have been caused by man, these widely separated countries would at once be recognized as constituting one great zoölogical region, occupied by similar forms of mammalian life. The beaver, bear, wolf, stag, moose, reindeer, bison, are some of the many connecting forms which, as Allen pointed out, constitute this a single zoölogical region, HOLARCTICA.

It is a striking fact that at the beginning of Eocene times we find a similarity which is nearly if not quite as close as that which prevails to-day. This similarity of Basal Eocene times is intensified in Lower Eocene times. Then, however, follows a long period of disunion in the forms and evolution of mammalian life, extending through the Middle and Upper Eocene, in course of which the mammals become so different on the two continents that a zoölogist would certainly mark them off into two entirely distinct zoölogical regions, namely, the Old World or PALÆARCTICA, and the New World or NEARCTICA.

But just when the divergence seems most extreme, there comes at the beginning of the Oligocene a fresh faunal reunion, perhaps even more close than the first. These periods of union and separation again recur. We thus have good ground for dividing the whole Cænozoic Period into a series of grand FAUNAL PHASES.

a. Faunal phases. — Another means of distinguishing these faunal phases, in addition to the continental separation and reunion of the mammals,

[1] Knowlton, F. H., The Stratigraphic Relations and Palæontology of the "Hell Creek Beds," "Ceratops Beds" and Equivalents, and their Reference to the Fort Union Formation. *Proc. Wash. Acad. Sci.*, Vol. XI, no. 3, 1909, pp. 179–238.

is in the struggle or competition which we observe between two great divisions of mammals, which are so distinct in their affinities and evolutionary stages that they may almost be set apart as two groups. These are:

I. Archaic primitive mammals, partly descended from ancestors of great antiquity in the Age of Reptiles; mostly without modern descendants.
II. Mammals with modern descendants and relationships, chiefly comprising ancestors of existing families.

The gradual dying out, or extinction, of the *archaic* in competition with the *modern* types thus affords a second important means of dividing the Cænozoic into faunal phases. A third means of distinguishing the faunal phases, and one which lends variety to the subject, is that, especially during periods of separation, several families independently evolve in Europe and North America respectively, without interchange by migration.

Through these three means we may clearly divide the Cænozoic into seven great faunal phases, as follows:

I. First Faunal Phase, Basal Eocene, archaic mammals only are known. (p. 102).
II. Second Faunal Phase, Lower Eocene, archaic and modern mammals intermingled (p. 112).
III. Third Faunal Phase, Lower to Upper Eocene. Europe and North America separated (p. 138).
IV. Fourth Faunal Phase, Oligocene. Archaic mammals extinct. Europe and North America reunited (p. 178).
V. Fifth Faunal Phase, Miocene. African mammals reach Europe and North America. Europe invaded from Asia (p. 242).
VI. Sixth Faunal Phase, Middle Pliocene. North and South America reunited (p. 304).
VII. Seventh Faunal Phase, Pleistocene. Widespread extinction. Fresh invasion of America by European mammals (p. 374).

b. The archaic mammals. — Nature deals in transitions rather than in sharp lines. We cannot circumscribe the archaic mammals sharply, nor be sure as yet that some of them did not give direct descent to certain of the modernized mammals. Yet the mammals of the Basal Eocene of both Europe and North America are altogether of very ancient type; they exhibit many primitive characters, such as extremely small brains, simple, triangular teeth, five digits on the hands and feet, prevailing plantigradism. They are to be collectively regarded as the first grand attempts of nature to establish insectivorous, carnivorous, and herbivorous groups, or unguiculates and ungulates. The ancestors or centers of these adaptive radiations date far back in the Age of Reptiles. At the beginning of the Eocene we find the lines all separated from each other but not as yet very highly specialized. The specialization and divergence of these archaic mammals con-

tinue through the Eocene Period and reach a climax near the top, although many branches of this archaic stock become extinct in the Lower Eocene. The orders which may be provisionally placed in this archaic group are the following:

Marsupialia.
  Multituberculata, Plagiaulacidæ.
Placentalia.
  Insectivora. Insectivores not as yet positively identified in the Basal Eocene.
  Tæniodonta. Edentates with enamel teeth.
  Creodonta. Archaic families of carnivores.
  Condylarthra. Primitive light-limbed cursorial ungulates.
  Amblypoda. Archaic, typically heavy-limbed, slow-moving ungulates.

This group is full of analogies, but is without ancestral affinities to the higher placentals and marsupials. There are forms imitating in one or more features the modern Tasmanian 'wolf' (*Thylacinus*), the bears, cats, hyænas, civets, and rodents of to-day, but no true members of the orders Primates, Rodentia, Carnivora, Perissodactyla, Artiodactyla have been discovered.

A remarkably interesting palæogeographic fact is the presence of many similar if not actually related mammals in South America in the Upper Cretaceous or Basal Eocene *Notostylops Zone* of Patagonia. Since other members of this archaic fauna of North America are positively and widely represented in the Basal Eocene of Europe, we have abundant proof of that striking faunal community or widespread distribution of similar forms of mammalian life in the latter part of the Age of Reptiles which has already been referred to (p. 95).

I. THE BASAL EOCENE LIFE OF EUROPE AND AMERICA

There is little doubt that the extinction of the large terrestrial and aquatic reptiles, which survived to the very close of the Cretaceous, prepared the way for the evolution of the mammals. Nature began afresh with the small, unspecialized members of the warm-blooded quadrupedal Class to slowly build up out of the mammal stock the great animals which were again to dominate land and sea. One of the most dramatic moments in the life history of the world is the extinction of the reptilian dynasties, which occurred with apparent suddenness at the close of the Cretaceous, the very last chapter in the "Age of Reptiles."

Close of the Age of Reptiles and Beginning of the Age of Mammals

We are fortunate witnesses of these great events as they followed each other at two widely distant points, namely on the northern coast of France and Belgium, and in the heart of the Rocky Mountain region in Wyoming and northern Montana.

Toward the close of the Age of Reptiles, in late Cretaceous times, sea and land still possessed a large reptilian fauna; the great marine ichthyosaurs and plesiosaurs had previously become extinct, but the giant sea lizards, or mosasaurs, still survived.

In Belgium, the very summit of the Cretaceous, the Danian or Mæstrichtian Stage,[1] a name given to the exposures around Mæstricht, records the existence in the seas of several mosasaurs, namely, the huge *Mosasaurus giganteus* and the lesser *Platecarpus*, as well as of great marine turtles. On land there wandered the tall herbivorous dinosaurs known as Iguanodontia (*Orthomerus dolloi* Seeley) and their enemies, the carnivorous dinosaurs (*Megalosaurus bredai* Seeley).

At the same time in the Rocky Mountain region, where the land animals only are known, there existed several kinds of dinosaurs. Chief among the herbivorous forms were the giant Iguanodontia (*Trachodon*) or "duckbill" dinosaurs, the great paired-horned Ceratopsia (*Triceratops*), and the armored ankylosaurs (*Ankylosaurus*). All these herbivorous forms were subject to attack by the giant carnivorous megalosaurs of the genus *Tyrannosaurus*. There were also smaller dinosaurs (*Ornithomimus*), cursorial, or of swift-running habit. These reptiles were in the climax of specialization and grandeur; they moved amidst a stately flora of palms and sequoias interspersed with bananas and fig trees, and a very rich deciduous tree flora of modern south temperate type.

A great many species of small mammals are known in these Upper Cretaceous dinosaur beds of the Rocky Mountain region. They are without exception of small size, and as compared with the reptiles, they are humble and inconspicuous forms.

We have no conception as to what worldwide *cause* occurred, whether there was a sudden or a gradual change of conditions at the close of the Cretaceous; we can only observe that the worldwide *effect* was the same: the giant reptiles both of sea and land disappeared. Reptiles are so sensitive to temperature that it is natural to attribute this extinction to a general lowering of temperature, or refrigeration, but the flora shows no evidence of this either in Europe or America; nor is there evidence of any great geographic cataclysm on the surface of the earth, for the plant life transition from one Age to the other in the Rocky Mountain region is altogether gradual and gentle.

Among the successive stages and formations in which this momentous change from Age to Age is recorded are the following:

[1] According to De Lapparent, Danian and Mæstrichtian are not synonymous; the Mæstrichtian, forming a part of the Aturian (or Upper Senonian), is *earlier* than the Danian.

	Rocky Mountains	*Belgium*	*France*
Age of Mammals	3. Lower Eocene, Wasatch	= 3. Upper Landenian	= 3. Sparnacian
	2. Basal Eocene, Torrejon	= 2. Lower Landenian	= 2. Upper Thanetian (Cernaysian)
	1. Basal Eocene, Fort Union, Puerco	=	1. Lower Thanetian
Age of Reptiles	1. Upper Cretaceous, Laramie	= Danian, Mæstrichtian	

First, it will be observed that the Upper Cretaceous Laramie of America is broadly regarded as of age equivalent with the Danian or Mæstrichtian of Europe, also that both are characterized by a rich reptilian fauna, marking the close of the Age of Reptiles.

Lying at the base of the Eocene or dawn of the Age of Mammals in America are the Fort Union or great lignitic formation of Wyoming and Montana, and the Puerco of New Mexico; the latter is partly a tuff formation.

These are both *continental* deposits which are regarded as of the same age as those sea border, or *fluvio-marine* deposits in northern Europe, which are placed in the Lower Thanetian stage.

We thus enjoy a contemporaneous picture of mammalian life as it existed along the northern coasts of France and Belgium and in the river valleys, flood plains, and lake borders of the newly born Rocky Mountain region of New Mexico and Montana. For it must be remembered (p. 93) that this region too had not long previously been on the borders of an inland sea.

Seashore transition beds in Europe. — The very ancient Basal Eocene formations of Europe are along the sea borders and are thus not favorable to the preservation of mammalian life; yet the rocks are full of interest as serving to illustrate how an ancient encroaching seashore may record both its own life and that of the land near by.

An especially clear sequence of these transition deposits is that recently described by Depéret [1] in northern France near Rheims. (1) Immediately overlying the Cretaceous are the *Sables blancs siliceux de Rilly*, white seashore sands of variable thickness containing many marine molluscs which are similar to those in the *Sables de Bracheux*, another Basal Eocene formation. (2) The overlying *Gravier marin de Cernay*, or seashore gravels of Cernay (erroneously called *'Conglomérat' de Cernay* by Lemoine), containing species of typical marine molluscs characteristic of the Upper Thanetian (*Pectunculus*, *Ostrea*, *Lucina*), is also a marine or shore formation, rich in the teeth of sharks. The remains of mammals represent those carried into the borders of a shallow sea through river currents; they are iden-

[1] Depéret, Relations stratigraphiques des Faunes des Cernay et de Meudon au Mont de Berru. *Soc. Géol. France*, Ser. 4, Vol. VI, 1906, pp. 442–443.

tical in age with the mammals of the celebrated *fauna of Cernay*, which contains the marsupial multituberculate, *Neoplagiaulax*. As the coast was rising, this deposit was overlaid by (3) a bed of coarse sands, clays, and lignites, which represents the beginning of the Sparnacian, of a thickness of 17 m.; near this level were found the bones of the giant bird *Gastornis*, described by Lemoine. The coast was still rising, so that superposed (4) is a lagoon or lacustrine formation of marls and limestones without fossils. Superposed again are the (5) *Sables et argiles ligniteuses* with a brackish water molluscan fauna of Sparnacian age; in these sands and clay-lignites (21 m. above the *Gravier marin de Cernay*), have been found limb bones of *Coryphodon* identical in size with the typical specimen found at Meudon (*Marnes de Meudon*).

These records of a sinking and rising Basal Eocene shore line near Rheims are paralleled by the Lower Landenian, a Basal Eocene marine phase of Belgium, probably of the same age as the Cernaysian of Rheims. (1) This marine littoral formation contains no mammals, but a number of very characteristic reptiles, as follows: the large lizard *Champsosaurus lemoinei*, of the same species as that found near Rheims in the typical Cernaysian, abundantly represented and beautifully preserved; *Lytoloma*, a marine, shore-living turtle with a very powerful mandibular symphysis, evidently adapted to crushing the littoral molluscs; the giant bird *Gastornis* has also been found here. (2) Surely resting on the Lower Landenian is a fluviatile formation attributed to the Upper Landenian stage, and represented at Orsmael and Erquelinnes, localities in Belgium widely separated geographically but containing the same fauna, the genera being provisionally identified as follows: *Coryphodon, Phenacodus, Dissacus, Hyænodictis, Decticadapis, Plesiadapis*, also a most important member of the Perissodactyla-Equidæ, provisionally identified as *Pachynolophus maldani*. It appears from this evidence that the Upper Landenian of Orsmael and Erquelinnes, containing *Coryphodon* and a true perissodactyl, is of more recent age than the Upper Thanetian or Cernaysian, and should be correlated with the lower Sparnacian of France, or the Wasatch of North America.

Continental transition beds in America. — The gentle transition from the reptilian to the mammalian Age is far more simply shown in the succession of continental depositions in northern Montana. The passage from the Laramie (Hell Creek beds) to the Fort Union, or Lignitic beds, is apparently continuous. The indications are that the late Cretaceous Laramie was a period of open country traversed by sand-bearing rivers. In the succeeding Basal Eocene, or Fort Union, there is evidence that large parts of Montana, Wyoming, Colorado, and the Dakotas were covered with dense coal- or lignite-forming forests. Vast stretches of subtropical and more hardy trees were interspersed with swamps where the vegetation was rank and accumulated rapidly enough to form great beds of lignite. Here were bogs in which bog iron was formed. Amid the glades of these forests there wandered swamp turtles, alligators, and large lizards of the characteristic genus *Champsosaurus*. Plant remains in the Laramie Hell Creek beds have also been found in the Fort Union at various localities; types common to the Upper Cretaceous and Basal Eocene formations are the fig (*Ficus*), banana (*Musophyllum*), palms similar to the sabal of

Florida (*Flabellaria sabalites*), horse-tail rushes (*Equisetum*), the soapberry (*Sapindus*), the hardy sequoias (*Sequoia*) and gingkos (*Gingko*), also the oak (*Quercus*), and sycamore (*Platanus*). The existence of this continuous similar flora, as determined by Knowlton,[1] through the transition from the

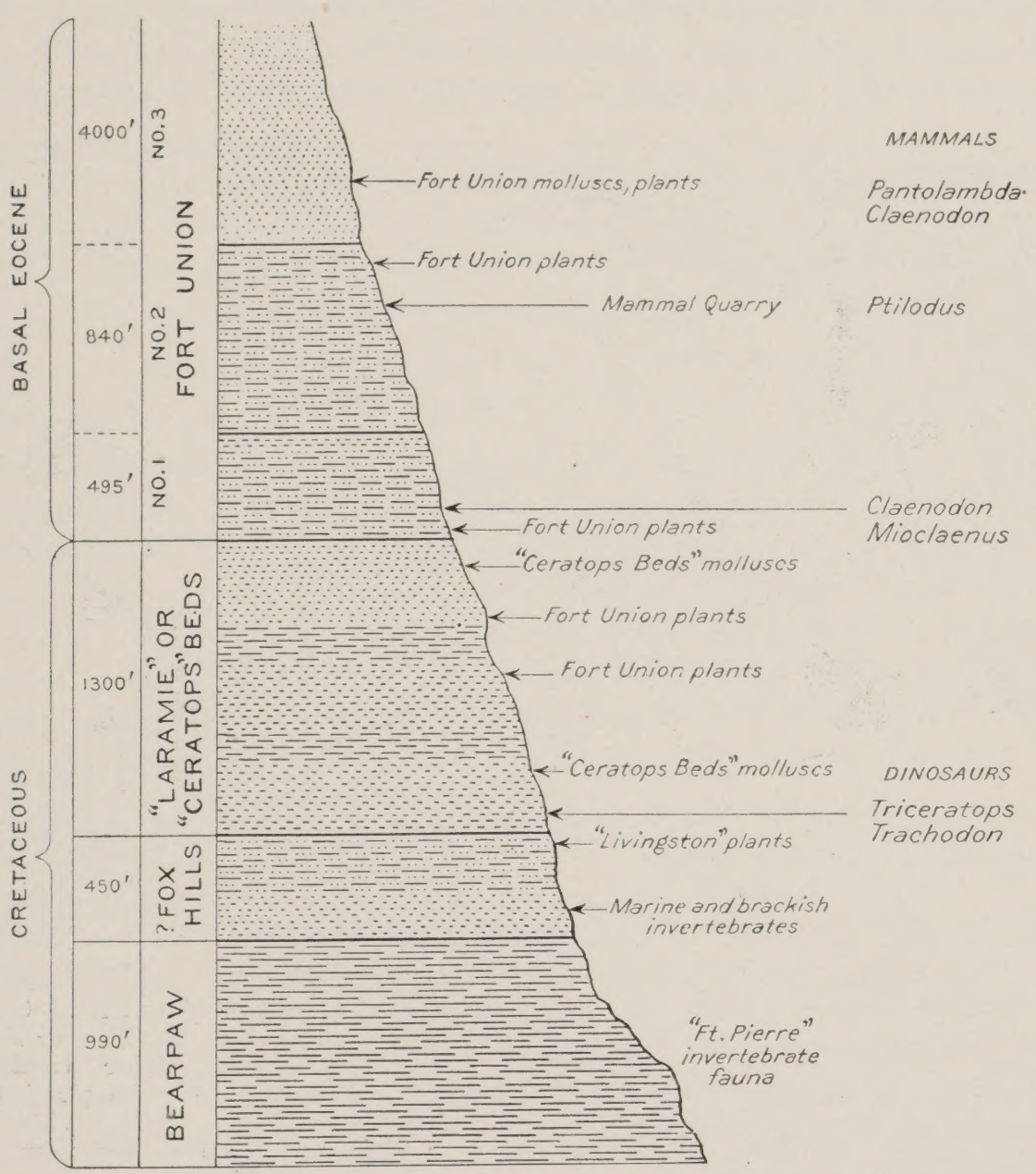


FIG. 25. — Age of Mammals succeeding the Age of Reptiles. Columnar section to the northeast of the Crazy Mountains, Montana, showing the Fort Union mammal beds (Basal Eocene), overlying the "Ceratops Beds" (Upper Cretaceous). Data of Stone and Stanton, 1910.

Age of Reptiles into the Age of Mammals, is strong evidence that the cause of the extinction of the Reptilia is not to be sought in a change of flora or in a lowering of temperature. A typical Basal Eocene mammalian fauna containing the marsupial Plagiaulacidæ is found as described below (p. 111).

[1] Knowlton, F. H., Notes on a Few Fossil Plants from the Fort Union Group of Montana, with Description of One New Species. *Proc. U.S. Nat. Mus.*, Vol. XVI, 1893, pp. 33–36; also, The Tertiary Floras of the Yellowstone National Park. *Amer. Jour. Sci.*, Vol. II, 1896, pp. 51–58. Knowlton and Stanton, Stratigraphy and Palæontology of the Laramie and Related Formations in Wyoming. *Bull. Geol. Soc. Amer.*, Vol. VIII, 1897, pp. 127–156.

I. BASAL EOCENE, FIRST FAUNAL PHASE — MAMMALS SOLELY OF THE ARCHAIC TYPE COMMON TO THE NEW AND OLD WORLDS

Animals of the First Faunal Zone. — The *Basal Eocene* life zones in both countries are sharply characterized by the extinction or absence of the giant reptiles, by the survival from the Cretaceous of the large swamp

Fig. 26. — **Basal and Lower Eocene.** Thanetian, Cernaysian, Lower Landenian. FRANCE. — Glauconie de **1** *la Fère* (Aisne), fluvio-marine deposits (6 meters). Gravier marin de **2** *Cernay*, near Reims (.5–7 meters). Sables et calcaires de **3** *Rilly*, near Reims, lacustrine. Sables de **4** *Châlons-sur-Marne* (Marne). Sparnacian, Upper Landenian. BELGIUM. — **5** *Erquelinnes*, near French boundary. FRANCE. — Argile plastique et lignites de **6** *Soissons* (Aisne), **7** *Guny*, **8** *Muirancourt*, near Paris. **9** *Saron*, near Ste. Maxence. **10** *Laon* (Aisne). **11** *Upper Cernay*, near Reims. Conglomérat de **12** *Meudon*, near Paris. Lignites de **13** *Vaugirard*, near Paris. Travertin de **14** *Sézanne* (Marne), a calcareous tuff rich in plants. ENGLAND. — Woolwich and Reading Beds, "plastic clay," of **15** *Dulwich*, **16** *Croyden*, near London, marine and estuarine (4–28 meters) sands and clays. Lower Ypresian. ENGLAND. — **17** *London* clay of **18** *Herne Bay* (Kent), **19** *Kyson*, north of Harwich, **20** *Harwich* (Essex), **21** *Isle of Sheppey*, mouth of the Thames, marine and estuarine deposit (over 500 feet maximum). FRANCE. — Marine deposits of **22** *Pourcy*, near Reims. Upper Ypresian. FRANCE. — In Marne, near Épernay : **22** *Chavot*, sables à terédines d'*Ay*, marine (3–4 meters), marnes de *Cuis*. Correlation of Depéret.

or fluviatile lizard *Champsosaurus* (of the order Choristodera or long-snouted Rhynchocephalia). In the Rocky Mountain region this animal is also found in the underlying Laramie formation. Its survival both in the Rocky Mountain region, in Belgium, and in France is one of the most distinctive features of the Basal Eocene, because it is apparently on the verge of extinction and does not reappear in higher levels.

This Basal Eocene stage is further distinguished by the presence of numerous diprotodont marsupial multituberculates of the family Plagiaulacidæ, and by many other very primitive mammals.

It is also distinguished by the absence of any mammals belonging to modernized families. These first make their appearance on both continents in the Lower Eocene (Wasatch) in what is known as the *Coryphodon Zone*, probably equivalent to the Upper Landenian of Belgium or the Sparnacian of France.

The chief distinction of this mammal fauna is that it represents a *survival* of the mammalian life of the Age of Reptiles, and so far as we know it now this life is all of the archaic type. We are, in fact, witnessing the close of a faunal phase which opened well back in Cretaceous times.

Basal Eocene of Europe

Thanetian Formation. — The Basal Eocene of Europe is known as the Thanetian Stage; it is named after the Isle, or promontory, of Thanet, at the mouth of the Thames. As above described on p. 99, it is divided into inferior and superior levels. In France it is typified by the fluvio-marine *glauconie de la Fère*, from which the single famous bear-like creodont *Arctocyon primævus* was described in 1841. With the superior level (Upper Thanetian) is paralleled the fluvio-marine gravel deposit of Cernay, near Rheims, from which the famous "fauna of Cernay" was described by Lemoine.[1]

Characteristic Mammals
Plagiaulacids
Adapisoricids
Lemuroids (?)
Insectivores, (?)
or Condylarths (?)
Arctocyonids
Oxyclænids
Triisodonts

This very rich Cernaysian or Upper Thanetian fauna is nearly of the same age as the Torrejon fauna of northern New Mexico; that is, its age is a little more recent than the underlying true Puerco fauna of New Mexico. It contains small insectivores, lemur-like mammals, a few hoofed mammals, and many carnivores. It is especially interesting to compare the teeth of *Neoplagiaulax* (Cernaysian) with those of *Ptilodus* (Torrejon) as in a similar stage of evolution; these are small, gnawing, diprotodont marsupials, which may be descended from *Plagiaulax* of the Upper Jurassic. The Insectivora are represented by members of the family Adapisoricidæ, somewhat analogous to the tree shrews (*Tupaia*). Primitive monkeys, possibly lemuroids, are represented by small animals referred to the Plesiadapidæ. More doubtful is the identification of the teeth of the herbivorous tuberculate pattern with that of one of the primitive cursorial ungulates (*Euprotogonia*) of the hoofed order Condylarthra of the Torrejon. *Pleuraspidotherium* somewhat resembles *Meniscotherium*, the primitive ungulate or condylarth of more recent

[1] See Lemoine, various papers listed in Bibliography.

geological age in the Rocky Mountains; it may as well be an insectivore. The comparison of the primitive carnivores or Creodonta in the two countries is closer, namely, of the Thanetian species of *Arctocyon*, with its omnivorous, bear- or raccoon-like teeth, with those of *Clænodon* of northern New Mexico. Similarly the Thanetian *Procynictis* parallels *Chriacus* of the American family Oxyclænidæ, and *Hyænodictis* is similar to the American *Dissacus* of the Mesonychidæ. Contrary to the recent opinion of Depéret, it does not appear probable that the presence is demonstrated of any of the modernized animals, *e.g.* artiodactyl or perissodactyl ungulates, in this imperfectly known fauna. Similarly we note the absence of, or have thus far failed to discover in this fauna any relatives of the Edentata (Tæniodonta) or Amblypoda,[1] both characteristic of the Torrejon. Of course the Cernaysian river deposit presents a very incomplete picture of the mammalian life of France during this period, for as observed by Lemoine and Depéret these mammal remains were only those which were washed into streams and carried to the sea near by.

The associated freshwater fishes of northern France and Belgium are related to the garpikes (*Lepidosteus*) and bow-fins (*Amia*), now met with only in the great rivers of North America. There are many turtles, all marsh and river varieties, Crocodilia, both of the crocodile, or Nile type, and the long-snouted, gavial type, of the Ganges. Extremely adapted to aquatic life is the rhynchocephalian lizard *Simædosaurus*, related to the *Champsosaurus* of the Basal Eocene of North America. The flightless bird *Gastornis*, belonging to the order of Chenomorphæ, according to von Zittel,[2] is remarkable for its huge proportions and its powerful legs in contrast with its feeble wings.

The flora of this Basal Eocene period indicates a moderately warm and temperate climate free from great extremes, including palms (*Flabellaria*), laurels (*Laurus*), cinnamons (*Cinnamomum*), and a doubtfully referred grass (*Poacites*).[3] In the extreme north the Basal Eocene flora[4] of Greenland, Iceland, and Spitzbergen included lindens, alders, magnolias, poplars, and birches, indicating a temperature similar to that of south temperate France or California at the present time.

Basal Eocene of North America

Puerco and Torrejon Formations. — In northwestern New Mexico, at the head of the Puerco River on the divide between the Rio Grande and San Juan rivers, are the Basal Eocene, post-Cretaceous beds which Pro-

[1] As above noted (p. 100), the inclusion in this stage of mammals found in the Upper Landenian of Orsmael and Erquelinnes, namely, Amblypoda (*Coryphodon*) and Perissodactyla (primitive Equidæ) is extremely doubtful.

[2] Von Zittel, Text-Book of Palæontology, transl. by Eastman, Vol. II, 1902.

[3] De Lapparent, Traité de Géologie, 1906, p. 1492.

[4] *Ibid.*, p. 1504, citation from Heer's Flora fossilis arctica.

fessor Cope described as "Puerco marls" in 1875,[1] and from which he listed the first mammalian fauna in 1881.[2] The formation overlies the Upper Cretaceous (Laramie) and underlies the Wasatch (Sparnacian, Ypresian).

In 1895 Wortman observed a natural subdivision of the formation into Lower or Puerco proper, and Upper or Torrejon, estimating the combined thickness at 800 to 1,000 feet.[3] In 1897 Matthew[4] separated the fauna of

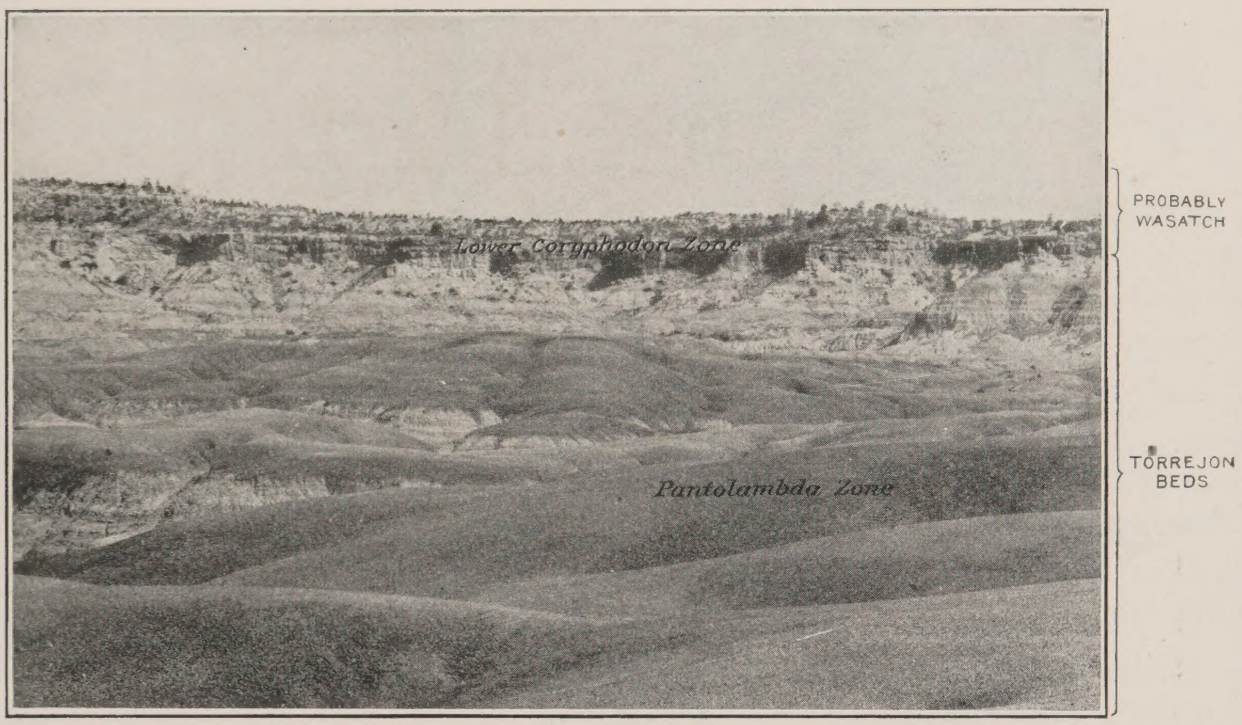


FIG. 27. — Badlands of northern New Mexico, head of Torrejon River. Basal Eocene, Torrejon-Pantolambda Zone below. Lower Eocene, Wasatch-Coryphodon Zone above. From photograph by American Museum of Natural History, 1896.

the two levels, adopting Wortman's proposed designation Torrejon for the upper beds, which are nearly of Upper Thanetian or Cernaysian age. As distinguished by its mammalian life this division is as follows:

UPPER: TORREJON FORMATION (300 feet), zone of *Pantolambda*, the earliest known member of the Ungulata-Amblypoda, with crescentic teeth, ancestral to *Coryphodon*.

LOWER: PUERCO FORMATION (500 feet), zone of *Polymastodon*.

In 1901 Douglass discovered in the Fort Union or great lignite formation of the upper Missouri River in northern Montana, a bed of shale con-

[1] Cope, E. D., Report on the Geology of Northwestern New Mexico, Examined During 1874, *Append. LL, Ann. Rept. Chief Eng.*, Washington, 1875.

[2] Cope, E. D., On Some Mammalia of the Lowest Eocene Beds of New Mexico. *Proc. Amer. Philos. Soc.*, Vol. XIX, 1881, pp. 484–495.

[3] Osborn, H. F., and Earle, Chas., Fossil Mammals of the Puerco Beds. Collection of 1892. *Bull. Amer. Mus. Nat. Hist.*, Vol. VII, Art. i, Feb., 1895.

[4] Matthew, W. D., A Revision of the Puerco Fauna. *Bull. Amer. Mus. Nat. Hist.*, Vol. IX, 1897, pp. 259–323.

taining a mammalian fauna of Torrejon age, including especially the condylarth *Euprotogonia* and the amblypod *Pantolambda.*[1]

Reptilian fauna. — Abundant remains of three different species of *Champsosaurus,* the large, aquatic lizard with a gavial-like snout, have been found in the Puerco. This animal (p. 100) occurs also in the Lower Eocene of France (vicinity of Rheims) and of Belgium. From the Puerco has been obtained also the earliest known North American serpent (*Helagris prisciformis*), unspecialized in character and of about the size of the common black snake (*Bascanium constrictor*).

FIG. 28. — Skull of the Basal Eocene plagiaulacid *Ptilodus* (× ⅔). In the U.S. National Museum, Washington. After Gidley.

Puerco Life of the New Mexico Region

Neoplagiaulax or *Polymastodon Zone.* — This is the earliest known of the Eocene mammal groups, immediately succeeding the Cretaceous, and preceding in age the Torrejon and Cernaysian. In New Mexico and Montana are found these small archaic mammals evolving from ancestors of the Age of Reptiles. Two of the genera date, in family ancestry (Plagiaulacidæ), as far back as the Upper Triassic or Rhætic, namely: of the diminutive multituberculates, (1) *Neoplagiaulax,* which represents a decided advance upon *Ptilodus* of the Upper Cretaceous (Laramie), and (2) *Polymastodon,* which similarly is much more modern than *Meniscoëssus* of the Laramie. The latter animal is as large as a beaver (*Castor*). In general these mammals were the marsupial rodents of the Mesozoic period.

[1] Douglass, E., The Discovery of Torrejon Mammals in Montana. *Science,* n.s., Vol. XV, 1902, pp. 272–273.

Two orders of archaic hoofed mammals, or ungulates, are known here, namely: (1) the Amblypoda, or short-footed forms, represented by the bunodont Periptychidæ, which receive their name from the sculptured sides of the grinding teeth of the type genus *Periptychus*. This family embraces a number of large and small herbivorous mammals, all with a peculiar triangular asymmetry in their superior molar teeth, of considerable range in size, probably in part arboreal in habit. (2) The light-limbed ungulates, or Condylarthra, are doubtfully represented by one genus (*Protogonodon*) of the family Phenacodontidæ. The gnawing or leaf-eating Herbivora of the order Tæniodonta are represented by two families, Stylinodontidæ and Conoryctidæ. This order is also known as Ganodonta (γάνος, enamel, ὀδούς, tooth), a name assigned by Wortman when he demonstrated that certain descendants of these mammals present many resemblances to the gravigrade South American edentates, although distinguished by the persistence of dental enamel, which has disappeared in all the true Edentata. Of doubtful affinity to the Insectivora are the two genera *Mioclænus* and *Oxyacodon*. The primitive carnivores, or Creodonta, of this phase have been discovered only in part. They include two families (Triisodontidæ, Oxyclænidæ), represented by five genera. By Wortman the Oxyclænidæ were regarded as Insectivora.

It is noteworthy that not a single representative ancestor of any *existing* order of mammals is certainly recognized in this assemblage. The possible exceptions are the supposed representatives of the Edentata and Insectivora, both very ancient orders. The opinion of Cope that the ancestry of modernized mammals was to be sought in these Puerco forms therefore lacks direct confirmation. The opposite opinion that the Puerco-Torrejon mammals are not ancestral to the modern mammals was developed by Osborn (1893-1904),[1] when he applied to them the name *Meseutheria*, indicative of their archaic or Mesozoic character.

Negatively, therefore, the Puerco is distinguished by the absence of recognizable primates, rodents, carnivores, and of any modern families of insectivores, artiodactyls, and perissodactyls. A summary of the Puerco mammalian fauna is as follows:

	Genera	*Species*
Archaic mammals of Triassic ancestry, Marsupialia Diprotodontia	4	5
Archaic mammals of Cretaceous ancestry	15	24
Mammals of modern affinity	0	0

Torrejon Life of the New Mexico and Montana Regions

Pantolambda Zone. — All the Mammalia of the Torrejon phase, or Pantolambda zone were found about three hundred feet above those of the

[1] Osborn, Rise of the Mammalia in North America, 1893; and Ten Years' Progress in Mammalian Palæontology, 1904. See Bibliography.

Puerco phase, and thus represent a very long interval of geologic time. They are of somewhat larger size, considerably more varied, and in the presence of one new family (Miacidæ, genus *Didymictis*) more modern. The diprotodont multituberculates, including the diminutive *Neoplagiaulax* and *Ptilodus*, and the much larger *Polymastodon*, still occur in this zone. Gidley [1] has recently made the most important discovery that the animal called *Chirox* by Cope [2] is actually the same as *Ptilodus* or *Neoplagiaulax;* that is, it represents the superior dentition; a beautifully preserved skull

FIG. 29. — Archaic hoofed mammals of the Pantolambda Zone. Outline restorations to same scale ($\times \frac{1}{16}$). *A. Meniscotherium*, a condylarth. (See also Fig. 39.) *B. Pantolambda*, an amblypod, short-footed, semi-plantigrade. *C. Euprotogonia*, a condylarth, long- and slender-limbed.

and part of the skeleton of *Ptilodus* found in the Fort Union of Montana demonstrates beyond question that this animal, and consequently all the multituberculates, are true marsupials, aberrant diprotodonts, as was originally surmised by Owen [3] in describing *Plagiaulax* from the Upper Jurassic. The chief peculiarity is that (Fig. 28) the upper and lower teeth are fundamentally different in numbers and in arrangement and do not oppose each other. Gidley is inclined to consider these animals as frugivorous, the incisors being well fitted for picking small fruits or berries. The previous view has been that they were gnawing types analogous to the rodents. It is important to note that these are the very last survivors of this very ancient family of plagiaulacids (Plagiaulacidæ).

As compared with the Puerco, the faunal summary is as follows:

	Genera	*Species*
Archaic multituberculates, Marsupialia Diprotodontia	4	4
Archaic or primitive mammals of Cretaceous ancestry	20	37
Modern, or possibly related to the modern Carnivora	1	1

[1] Gidley, J. W. Notes on the Fossil Mammalian Genus *Ptilodus*, with Descriptions of New Species. *Proc. U.S. Nat. Mus.*, Vol. XXXVI, June 19, 1909, pp. 611–626, Pl. 70.

[2] Cope, E. D., *Proc. Amer. Philos. Soc.*, Vol. XXI, 1883, p. 321.

[3] Owen, R., Monograph of the Fossil Mammalia of the Mesozoic Formations. *Mon. Pal. Soc.*, 1871.

Thus the archaic forms predominate in the ratio of forty-one species of archaic to one species of modern affinities. This rich fauna is believed to be of the same age as that of a portion of the Fort Union of Montana, as described by Douglass [1] (1902) and Farr. Its approximate parallels in Europe (Upper Thanetian or Cernaysian) are indicated by the common presence in France and North America of somewhat similar stages of evolution among the representatives of three or four families, namely: (1) Plagiaulacidæ, (2) Arctocyonidæ, (3) Mesonychidæ-Triisodontinæ, (4) Oxyclænidæ. As noted above, other identifications of the Torrejon and Cernaysian faunas are somewhat uncertain.

As in the Puerco, these Torrejon mammals belong almost exclusively to an older radiation, destined to become extinct during the Eocene. This elimination, in fact, begins at once, because five out of the fourteen families of mammals discovered in the Torrejon make their last appearance at this stage. The remark applied by Dr. Lemoine to the Cernaysian fauna, "*Comme c'est drôle, ce monde là,*" certainly applies with equal force to the Torrejon world; it was certainly strange and *bizarre,* none the less extremely interesting and fortunately much more completely known than the Puerco assemblage, because the limbs and feet of several of its members have been discovered.

It was the happy finding of the fore foot of *Psittacotherium* which led Wortman [2] to the demonstration that this member of the family Stylinodontidæ, as well as the animal known as *Conoryctes* of the order Tæniodonta (Ganodonta), are strongly analogous if not actually related to the South American gravigrade Edentata, such as *Megalonyx,* and the armadillos, respectively.

These browsing or leaf-eating tæniodonts now attain a considerable size, and present a direct passage between the *Wortmania* ("*Hemiganus*") of the Puerco and the *Calamodon* of the Wasatch or Sparnacian. There are still no true rodents. Beside the Mioclænidæ (*Mioclænus*) and Pantolestidæ (*Pentacodon*) there are the Mixodectidæ, making their first appearance with a pair of greatly enlarged incisor teeth, which suggested to Cope their affinity with the *Chiromys,* or Aye-Aye, of Madagascar, and to Osborn their possible relationship to the Rodentia (Order Proglires). These small insectivore, rodent, or lemur-like forms are destined to survive to the summit of the Eocene.

It is noteworthy how frequently *diprotodonty,* or the enlargement of a front pair of incisor teeth, appears not only in the marsupial suborder 'Diprotodontia,' but as a parallel or analogous adaptation in these Basal Eocene mammals of Europe and America, and in the several families of other orders.

[1] Douglass, E., A Cretaceous and Lower Tertiary Section in South-Central Montana. *Proc. Amer. Philos. Soc.*, Vol. LXI, 1902, pp. 207–224.

[2] Wortman, J. L., The Ganodonta and their Relationship to the Edentata. *Bull. Amer. Mus. Nat. Hist.*, Vol. IX, 1897, pp. 59–110.

Of the archaic ungulates, the light-limbed Condylarthra are now certainly represented by two genera of Phenacodontidæ (*Tetraclænodon, Euprotogonia*), the former reported both from New Mexico and Montana. Of the slow-moving Amblypoda the bunodont Periptychidæ are still represented by four genera, and the selenodont Pantolambdidæ, which are considered more nearly ancestral to the coryphodonts of the Wasatch, make their first appearance. The genus *Pantolambda*, including animals rang-

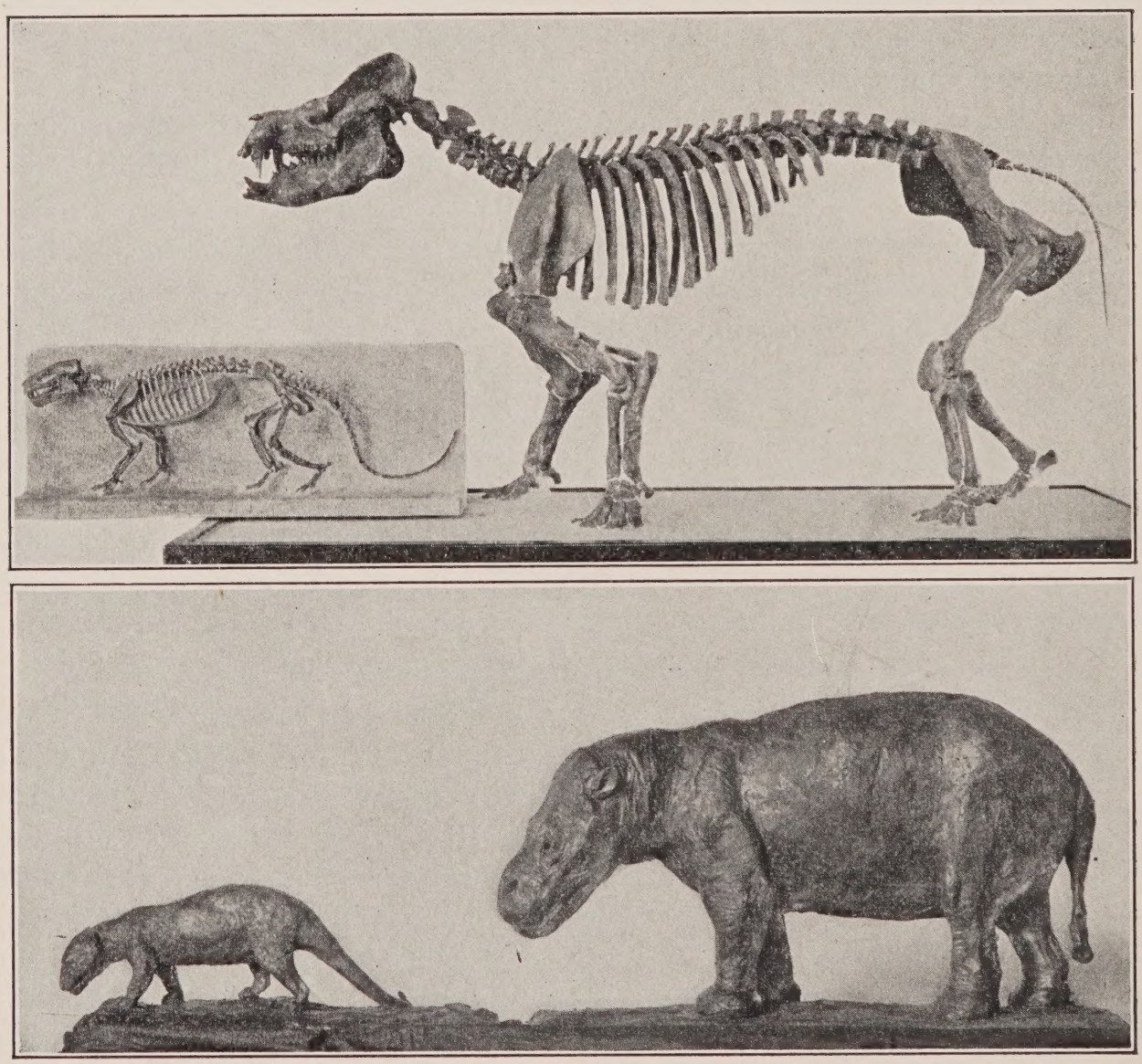


FIG. 30. — Basal and Lower Eocene stages in the evolution of the heavy-limbed Amblypoda. Above : Skeletons of the small *Pantolambda* and its large successor *Coryphodon*. Below : Restorations of the same by Charles R. Knight. Both in the American Museum of Natural History.

ing in size from that of a large beaver to that of a sheep, receives its name from the lambda shape of the cusps of its superior grinding teeth; out of these simple cusps were destined to arise the extraordinary yoke-shaped teeth of *Coryphodon* and the still stranger crested teeth of *Uintatherium*. The primitive skull, short limbs with everted elbows, the short, spreading feet and long tail of this animal, all point toward ancestry from an unguiculate or clawed animal of the primitive carnivore-creodont build.

It should be noted that there are no lemurs or other primates certainly recognized in this fauna. Several of the animals which were regarded as lemuroid by Cope are now placed near the insectivores (Matthew, 1909).

PREVAILING MAMMALS
Plagiaulacids
Periptychids
Pantolambdids
Phenacodonts
Tæniodonts
Mixodectids
Insectivores (?)
Pro-Carnivores (or Creodonts)
Triisodonts
Oxyclænids
Arctocyonids

The ancient Carnivora (Creodonta) are either richer or more fully known in this phase than in the Puerco, since they are represented by four families, Arctocyonidæ (*Clænodon*), Mesonychidæ (*Dissacus*), Triisodontidæ (*Sarcothraustes*), Oxyclænidæ (*Chriacus, Tricentes, Deltatherium*). These creodonts are partly provided with tubercular teeth, partly with subtrenchant or cutting teeth. It is important to observe that no well-developed sectorial teeth have as yet evolved in this phase; in other words, the Creodonta are not yet perfected as flesh eaters.

The first rudiments of modernism are seen in the genus *Didymictis*, a member of the family Miacidæ, which may be considered one of the true pro-Carnivora because in the disposition of its carnassial or sectorial teeth it agrees with dog-like and civet-like forms of the higher Wasatch and Bridger Formations.

II. THE LOWER EOCENE LIFE OF EUROPE AND AMERICA

We now enter the life or faunal zone of *Coryphodon*, the bulky successor of *Pantolambda*, an animal known both in Europe and North America; also of *Hyracotherium* and *Eohippus*, the first representatives of the horses (Equidæ). Depéret (see p. 100) was of the opinion (1905) that *Coryphodon* and *Hyracotherium* appear earlier in Europe than in America, namely, in the Lower Landenian of Belgium, which he synchronizes with the Cernaysian[1] or Thanetian; the evidence for this correlation does not appear conclusive. It is quite possible, however, that both *Coryphodon* and the primitive horses may be found at an earlier geological phase in the Old than in the New World. In whichever continent the coryphodons and horses did originate, there is no doubt as to the occurrence of a sudden modernization, through the appearance both in Europe and North America of an assemblage of mammals, unheralded by ancestral forms, which includes ancestors of four or five modern orders and embraces eleven new families, two of which persist to the present time and none of which have been observed in the Torrejon or Puerco phases. We are thus in another of the great successive faunal phases, namely, the Second, as follows:

[1] Depéret, C., L'évolution des Mammifères tertiaires; importance des migrations (Eocène). *C. R. Acad. Sci. Paris*, Vol. CXLI, séa. Nov. 6, 1905, p. 702.

II. LOWER EOCENE, SECOND FAUNAL PHASE — FIRST MODERNIZATION IN EUROPE AND AMERICA, OR INVASION OF ANCESTORS OF MODERN MAMMALS WHICH MINGLE AND COMPETE WITH ARCHAIC. CLOSE FAUNAL CONNECTION BETWEEN WESTERN EUROPE AND WESTERN NORTH AMERICA. APPARENT BREAK BETWEEN NORTH AND SOUTH AMERICA. INITIAL ELIMINATION OF ARCHAIC IN COMPETITION WITH MODERN MAMMALS.

European palæontologists have usually attributed the source of the modern families of the Second Faunal Phase to North America; while this theory is without evidence, it is certain that this fauna originated neither in South America nor in Africa. There remain four possible centers of

FIG. 31. — Coryphodonts, typical, large mammals of the Lower Eocene. To the left a coryphodon bull with large tusks; to the right a cow, with small tusks. After the original by Charles R. Knight in the American Museum of Natural History.

origin, namely: (1) the Great Plains and Atlantic Border region of North America; (2) the more northerly American Mountain Region, that is, British Columbia; (3) the northerly American-Asiatic land mass or northern Holarctica; (4) the northerly Eurasiatic region or northern Palæarctica. Each of these regions was sufficiently large and varied to give origin to a diversified modern fauna, but in the writer's judgment the nearly simultaneous appearance in western Europe (latitude 50°), and in North America (latitude 40°), favors the fourth hypothesis, namely, that these mammals had been previously developing in the northerly portion of Holarctica, or in the North-American-Asiatic land mass. There was certainly such a

great land mass to the north, of warm to temperate climate favorable to the evolution of these higher forms of mammalian life; in fact, there is every reason to believe that this northerly region was throughout the whole pre-Pleistocene Cænozoic period highly favorable to the evolution and migration of the higher forms of the Mammalia. This, as seen in a north-polar view of the earth, was the area of the great migrating routes and must have enjoyed a favorable climate, otherwise the faunal continuity between Europe and western America could not have been so frequently renewed or sustained by intermigration. As detailed on p. 66, this hypothesis of a northerly or circumpolar center has been advocated by Wortman and others. It must be remembered, however, that the actual center from which these modernized mammals suddenly spread into Europe and North America is still hypothetical and will not be determined until the Basal Eocene fossil mammal beds in the unknown portions of America and Asia shall have been discovered.

Placing in contrast the archaic and modern orders in North America during the *Second Faunal Phase*, they appear somewhat as follows:

Archaic Orders	*Modern Orders*
Creodonta, creodonts	Carnivora, fissipede carnivores
Insectivora, insectivores	Rodentia, rodents
Tillodontia, tillodonts	Perissodactyla, odd-toed ungulates
Tæniodonta, ganodonts	Artiodactyla, even-toed ungulates
Condylarthra, phenacodonts	Primates, lemuroids or monkeys
Amblypoda, coryphodonts	

As noted above, the division is very arbitrary; the archaic or modern columns will be swollen or diminished by the respective transfer of the primitive Insectivora to the modern column, or of the primitive Lemuroidea to the archaic column.

Lower Eocene Life of Europe

As compared with that of America the Lower Eocene of Europe is more precisely subdivided at the present time by Depéret[1] and others through the alternation of marine and terrestrial formations, upon which the European palæontologist relies, while his American confrères are dependent entirely upon the freshwater phases of the Rocky Mountain basins. After it has been possible to make very close comparisons between the evolution stages of a large number of related mammals on the two continents, closer correlations may be made than are at present practicable. It is therefore best to treat Europe and America separately, first noting the broad parallelism of stages, as follows:

[1] Depéret, L'évolution des Mammifères tertiaires, etc. (Eocène), 1905.

Europe	*North America*
Upper Ypresian	Lower Bridger
	Huerfano (Upper)
Lower Ypresian	Wind River, Coryphodon Zone
	Upper Wasatch " "
	Huerfano (Lower) " "
Sparnacian	Lower Wasatch, Coryphodon Zone

Sparnacian Life, Coryphodon Zone

Sparnacian formations. — The Sparnacian Stage is broadly parallel with the Lower Wasatch of America; it receives its name from Épernay (Latin, Sparnacum). As shown in localities 6–16 of the accompanying map (Fig. 26), the chief formations representing this stage are along the old Suessonian coastline of northern France and southeastern England, formerly near the shoreline of the ancient North Sea, which is known geologically as the Suessonian Sea. The open Thanetian sea of the preceding phase is now succeeded by lagoons and estuaries, favorable to the formation of plastic clays and lignites. The typical deposits, *argiles plastiques et lignites de Soissons*[1] of lacustrine origin (6), are paralleled by the fluviatile *Conglomérat de Meudon* (12), near Paris, by the *Sables et argiles ligniteuses*, near Cernay (described above on p. 100), and by the *Travertin de Sézanne* (14) and the Woolwich and Reading Beds. The last two (15) apparently both yield a rich representation of the flora of the period. De Lapparent describes the Sparnacian as a period of fluvio-marine deposition, the region of Paris being occupied by a lagoon, while farther south were lakes.

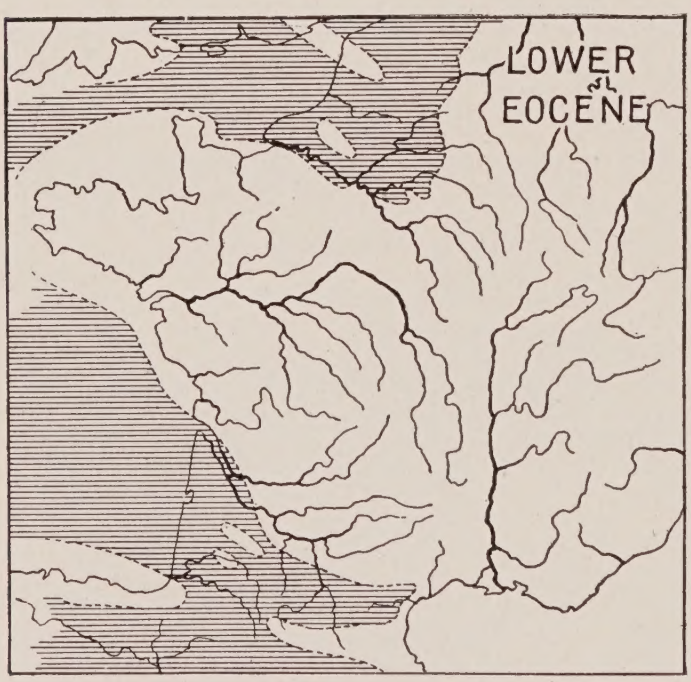


FIG. 32. — France in Lower Eocene, or Ypresian times. After de Lapparent, 1906. White = land. Ruled lines = sea. The modern river courses, as indicated, differ totally from those of Eocene times.

The lacustrine *Travertin de Sézanne* (a calcareous tuff), near the present site of Paris, includes the sassafras and other large trees of the laurel family, lindens and magnolias.[2] Similarly in the Woolwich Beds of southeastern

[1] The town, *Soissons*, is in Dept. Aisne, northeast of Paris.

[2] De Lapparent, Traité de Géologie, 1906, p. 1495.

England are found locusts (*Robinia*), figs (*Ficus*), tulip trees (*Liriodendron*), and *Grevillea*, a proteaceous plant now confined to Australia.[1] The marine and estuarine plastic clays of this formation also contain remains of *Crocodilus* and of the giant bird *Gastornis*.

PREVAILING MAMMALS
Coryphodonts
Hyracotheres (Horses)
Lophiodonts
Palæonictids

The remains of mammals are very scarce. In the Soissons deposits (6) are found three very important and distinctive forms, namely, the two heavy-bodied ungulate coryphodons *C. eocenus*, *C. oweni*, the former described in 1846 by Owen, the latter by Hébert ten years later. An equally significant form from the *Lignites de Soissons* is the odd-toed or perissodactyl ungulate *Lophiodon larteti*, which Filhol regarded as the ancestor of the true heavy-bodied lophiodonts.[2] Among the carnivorous mammals is the creodont *Palæonictis gigantea* (from Muirancourt, Oise, 8), a member of the Palæonictidæ, a family of cat-like, short-faced creodonts, which also appear for the first time in the Wasatch of the Rocky Mountains (*Palæonictis occidentalis*). In the Soissonais of Europe has also been found a large mesonychid creodont, *Pachyæna boulei*. Both at Meudon and in the upper deposits near Cernay are found the bones of *Coryphodon oweni*. This sparsely known mammalian fauna of Europe has its complete counterpart in the Rocky Mountain region.

From the Upper Cernay deposits near Rheims (see p. 100) (*sables et argiles ligniteuses*) is also recorded a femur (length .390) of *Coryphodon oweni* Hébert identical in size with the typical specimen found at Meudon.

Ypresian Life

Lower Ypresian formations. — The Ypresian stage is named from Ypres, Flanders. It is typified by the famous estuarine formation of the London Clay (166 m.), which is also the type of the *Étage Londinien* of Mayer-Eymar, a formation containing several important primitive mammals and marine molluscs, which prove that this is on a higher level than the Sparnacian. Exposures are at Herne Bay, Kent (18), Kyson (19), Harwich, Essex (20). Of the same age are the plant deposits of the Isle of Sheppey (21), near the mouth of the Thames, and the marine deposits of Pourcy (22) near Rheims. (See map, p. 102).

The mammals of the London Clay include the amblypod *Coryphodon eocenus*, also a small mammal *Platychœrops* (= *Miolophus*), an animal often compared with but certainly not related to the tillodont *Esthonyx* of the Rocky Mountain region; it is of the size of the marten (*Mustela*) and of

[1] Gardner, British Eocene Flora, *Palæont. Soc.*, p. 29, quoted by A. Geikie in A Text-Book of Geology, London, 1893.

[2] Depéret, C., Les Transformations du Monde animal (Paris, 1907), traces the evolution of the four phyla of lophiodonts from the Upper Ypresian stage (pp. 206–208).

uncertain relationships. The carnivore *Argillotherium* (Davies, 1884) is also indeterminate.

Horses. — Fortunately the primitive four-toed horses (Equidæ) are represented by several highly characteristic specimens of the genus *Hyracotherium* (=*Pliolophus*). The great English anatomist Owen [1] described these specimens (*H. leporinum* and *H. cuniculus*), but quite naturally failed to recognize their ancestral relationships to the horses. The type (*H. leporinum*) exhibits simple grinding teeth (Fig. 2) which are similar to those of *Eohippus borealis* of the Wasatch and Wind River Formations of the Rocky Mountains, but the second superior premolar tooth is a very simple, two-rooted, single-cusped tooth, whereas in all the American equines the same tooth is more complex, namely, invariably three-rooted and three-cusped, or with two external cusps and an internal ledge. This London Clay type of

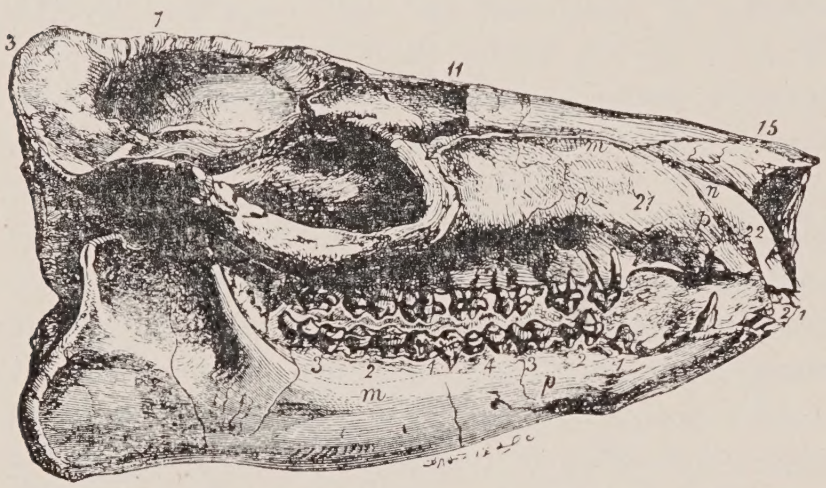


FIG. 33. — Skull of the primitive Eocene horse *Hyracotherium* (*Pliolophus*) *vulpiceps* of the London Clay ($\times \frac{1}{2}$). After Owen.

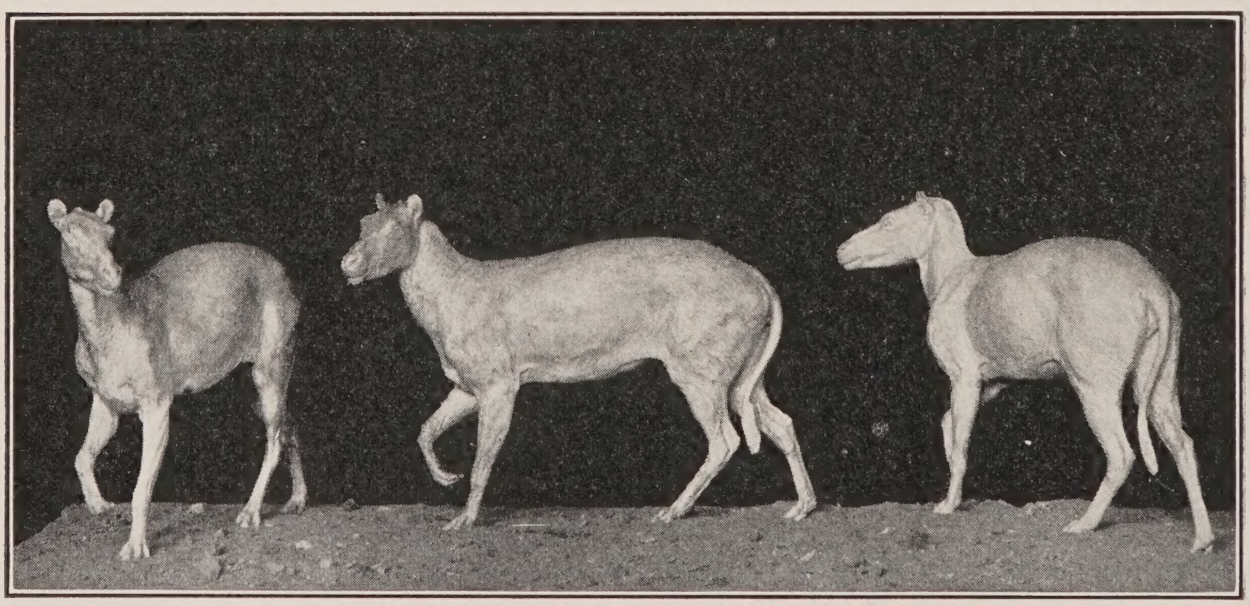


FIG. 34. — Models of the Lower Eocene, primitive horse of North America, *Eohippus*. After originals by Charles R. Knight in the American Museum of Natural History.

Hyracotherium, therefore, is the most primitive horse certainly known, and bespeaks the very early entrance of the horses into Europe. *H. vulpiceps*, or the 'fox-headed' hyracothere, also from the London Clay (see

[1] Owen, R., *Trans. Geol. Soc.*, Vol. VI, 1839 (1841), p. 203, and *Ann. Nat. Hist.*, Vol. VIII (1841), 1842, p. 1.

Fig. 33), is a somewhat more progressive horse, and is similar in its stage of evolution to the *Eohippus validus* of the Rocky Mountain region, which has the simplest fourth superior premolar of any of the American hyracotheres. We note especially the swelling brain case of these little horses (Fig. 33), indicative of a comparatively well-developed cerebrum. This London Clay phase is evidently of the Coryphodon Zone, broadly corresponding with the Wasatch, but possibly a shade older.

Fortunately our knowledge of the contemporary fish, reptile, and bird life is quite extensive. The fishes of the London Clay include rays (*Myliobatis*), sharks (*Odontaspis, Lamna*), sun-fishes (*Tetrapterus*), and saw-fishes (*Pristis*). Among the reptiles are marine and freshwater turtles and tortoises (*Chelone, Trionyx, Platemys*), two species of crocodile, and a sea-snake (*Palæophis*) of large size. Among the birds are *Steganopodes*, allies of the pelicans and cormorants; *Dasyornis*, also, a giant bird possibly allied to *Gastornis*, has been discovered.[1]

Of still greater interest is the rich land flora preserved in the Isle of Sheppey deposits near the mouth of the Thames.[2] This gives by far the best picture we have both of the environment and temperature of the most remote period of the horse. We find palms (*Nipa, Sabal, Chamærops*), conifers (*Sequoia, Pinus, Callitris*, now of Africa), the plantain (*Musa*), now confined to eastern Asia, the eucalyptus (*Eucalyptus*), now characteristic of Australia, the tupelo (*Nyssa*) now exclusively North American. There are also oaks, laurels, sweet gums (*Liquidambar*), magnolias, almonds (*Amygdalus*), and soapberries (*Sapindus*), altogether a flora south temperate rather than subtropical.

CHARACTERISTIC MAMMALS

Dichobunids (Artiodactyls)
Hyracotheres (Horses)
Lophiodonts
Insectivores
(?) Lemurs
(?) Mesonychids

Upper Ypresian Formations. — While the Lower Ypresian is in the Coryphodon Zone and corresponds in age with the American Wasatch and Lower Wind River depositions or close of the Lower Eocene, the Upper Ypresian lacks *Coryphodon* and contains a more recent fauna which, as Depéret observes, approximates it more closely to the Middle Eocene. It thus perhaps corresponds to the Upper Huerfano and base of the Bridger Formations of the Rocky Mountain region. The typical stage is locally known as the *Sables à Teredina personata*, especially exposed in northern France near Épernay, at Chavot (22), a marine formation, at Ay (22), and at Cuis. These are the *Sables agéiens* of Lemoine.

These *Teredo* sands contain the *faune agéienne* of Lemoine, which partly

[1] Geikie, A., Text-Book of Geology, 1893, p. 973; and Boyd Dawkins, Early Man in Britain, 1880, p. 19.

[2] J. S. Gardner's British Eocene Flora (*Paleont. Soc.*, p. 12), as quoted by A. Geikie, 1893, p. 973.

includes a continuation of the old mammals of the Upper Thanetian (Cernaysian), and partly a number of mammals now recorded or observed for the first time. Among the former is the insectivore *Adapisoriculus*, possibly related to *Adapisorex* of the Cernaysian, *Plesiadapis*, which resembles *Mixodectes* of the American Torrejon in its diprotodont dentition. The skull and skeletal characters do not agree well with those of modern insectivores, nor are they distinctively primate (Matthew). *Protoadapis* also appears, and like *Plesiadapis* is of doubtful primate reference; it has been classed with the Rodentia, or may be placed with *Mixodectes* among the *Proglires*. Creodonts are represented by *Hyænodictis*, allied to the mesonychids in tooth structure; the rodents by *Decticadapis* and *Plesiarctomys*. The odd-toed Ungulata are represented by two out of four great branches or phyla of the Lophiodontidæ which are destined to play a great part in the Eocene mammal life, namely, by the more robust form *Lophiodon remense* (of about the size of a tapir and ancestral to the great *L. lautricense* of the Upper Eocene) and by *Chasmotherium*, a small lophiodont lacking the third lobe of the last lower molar (ancestral to the *C. cartieri* of the Upper Eocene). These chasmotheres are of small size, the premolar teeth rapidly complicating; they tend to be short-headed, or brachycephalic, the teeth finally forming a closed series. The other phylum parallels the more robust lophiodons and survives until the close of the Middle Eocene. Depéret considers the '*Propachynolophus*' *gaudryi* (Lemoine) of these beds as a member of the Equidæ, but in the present writer's opinion the advanced condition of its grinding teeth, its considerable size, the presence of a mesostyle in the grinding teeth above and of a metastylid below appear to liken it rather to a primitive palæothere (?*Plagiolophus*). The smaller *Propachynolophus maldani* (the type of this species and genus), however, may be truly a hyracothere, or primitive horse. The Artiodactyla are now for the first time represented by the small pro-ruminant form *Protodichobune*.

Altogether the affinities of these animals await solution by much further study and comparison.

In deposits alleged to be of Upper Ypresian age in southeastern Europe (Transylvania) are found the remains of a large quadruped (*Brachydiastematherium*) related to the American family of titanotheres (see p. 556). This animal is in an Upper Eocene stage of evolution comparable to that of the American *Protitanotherium* (p. 169). It thus appears probable that these deposits are much more recent than Lower Eocene.

Lower Eocene, Wasatch and Wind River Life of North America

The Lower Eocene of North America is the great *Coryphodon Zone;* it is represented by a grand fauna known from thirty-eight years of exploration in formations which are broadly known as "Wasatch," this

being the name first applied by Hayden[1] to a group of beds of this age near Evanston, western Wyoming. This Evanston 'Wasatch' represents the earliest phase (corresponding with the Sparnacian and Lower Ypresian of Europe), a more recent phase of the same fauna being contained in the Wind River Formation of central Wyoming. The animals which tie these vastly extended deposits together are *Coryphodon*, *Eohippus* (the earliest type of American horse), *Phenacodus*, and *Palæonictis*. In the Wind River (corresponding with the Upper Ypresian of Europe), *Bathyopsis*, a new member of the Order Amblypoda appears.

The contrast which the life of the Coryphodon Zone of the Wasatch and Wind River exhibits to the very archaic and chiefly Mesozoic fauna of the underlying and earliest Torrejon and Puerco formations (p. 111) renders this one of the most striking of modernizations in the whole American Cænozoic.

The archaic and modern mammals are in these North American Sparnacian and Lower Ypresian beds thoroughly mingled; the former still predominate in the number of genera and species; they also predominate in size, *Coryphodon* and *Phenacodus* and the carnivorous creodonts being the largest mammals of the period.

The mammals belonging to the modernized orders are inferior in size and in number of species, but prove to be mechanically superior both in their foot and tooth structure, and of higher intelligence.

The summary of this mingled fauna is as follows:

Summary of Wasatch Genera and Species

	Genera	*Species*
Multituberculate marsupials (Plagiaulacidæ)	0	0
Placental mammals of archaic type	18	48
Placental mammals with modern affinities	11	33

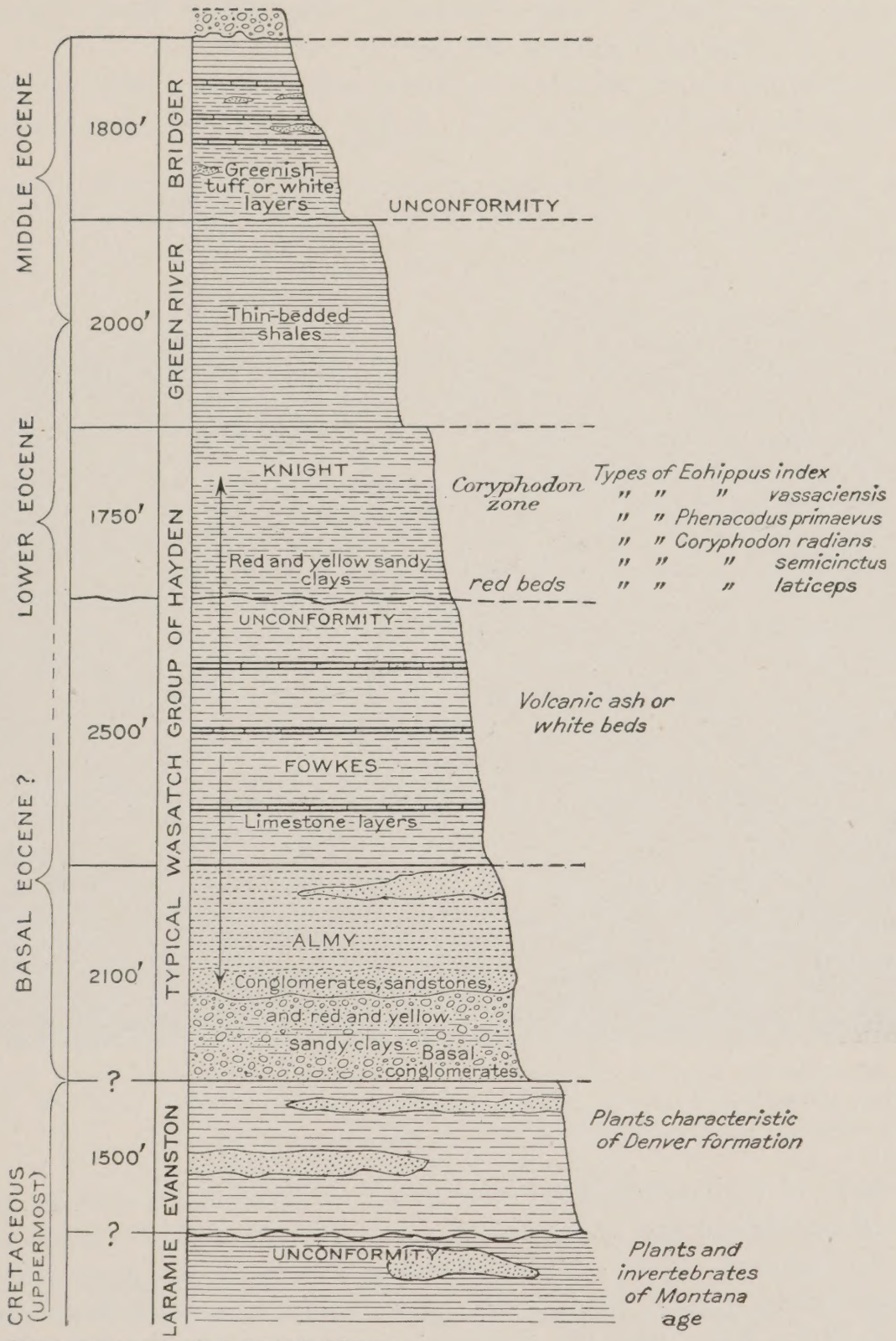
In this calculation the Insectivora are included among the archaic forms, the Primates, or Lemuroidea, among the modern. Naturally a sharp line cannot be drawn between orders, and the above table only represents the momentous change in a broad way. As compared with the summaries on pp. 107–8, the contrast is sufficiently striking.

Formations of the Coryphodon Zone. — Phase I. As shown in the accompanying map, the chief exposures in the central Rocky Mountain region are as follows: (1) the typical 'Wasatch' group of Hayden, or more restrictedly the 'Knight Formation' of Veatch, 1,750 feet; (2) the Wasatch of the Black Buttes (= Bitter Creek of Powell, = Vermillion Creek of King, 1878), in the Washakie Basin, Wyoming; (3) the 'Wasatch' of the

[1] Hayden, F. V., Geological Report of the Exploration of the Yellowstone and Missouri Rivers, by F. V. Hayden, assistant to Col. William F. Raynolds, U. S. Engineers, Washington, 1869.

By permission of the U.S. Geological Survey.

FIG. 35. — Heart of the ancient Eocene flood plain and lake region of Wyoming, showing the areas of Eocene deposition which have resisted erosion. **Lower Eocene:** Wasatch (oblique lines); Wind River (horizontal lines); Green River (vertical lines). **Middle Eocene:** Bridger and Washakie (horizontal lines). **Upper Eocene:** Uinta (horizontal lines).



By permission of the U.S. Geological Survey.

Fig. 36. — Scale section of the Lower and Middle Eocene of southwestern Wyoming, showing the relations of the "typical Wasatch group" of Hayden (*A*); Modified from Veatch, 1907.

San Juan Basin of northern New Mexico, 1,500 feet, overlying the Torrejon and Puerco series; (4) the 'Wasatch' of the Big Horn of Wyoming, 2,391 feet (Loomis). *Phase II.* (1) The lower portion of the Huerfano Formation near Spanish Peaks, Colorado. The Wind River Formation (Hayden) of northern Wyoming, 500 feet.

These formations all contain *Coryphodon* and *Eohippus*, and may be collectively known as Lower Eocene. Below them were either mammalif-

Fig. 37. — In the heart of the Lower Eocene badlands on Gray Bull River, Big Horn Basin, Wyo. Wasatch Formation. Zone of *Coryphodon*, primitive horses, tapirs, etc. Photograph by American Museum of Natural History, 1896.

erous beds of undoubted Basal Eocene age (Puerco and Torrejon) or deposits of equivalent age (*e.g.* Fowkes, Almy, Fig. 36, p. 119) resting on the Upper Cretaceous. The fact of paramount interest is the great thickness of these Lower Eocene depositions, amounting in western Wyoming to 4,000 or 5,000 feet. For the beds which intervene between this Coryphodon Zone and the summit of the Cretaceous, the thickness indicates an enormous period of time, ample even for the transformation of the diminutive ancestors of *Pantolambda* into the bulky *Coryphodon* (Figs. 30 and 31).

The materials of which these various deposits of the Coryphodon Zone

were composed are partly indicated in the petrographic analysis of Johannsen.[1]

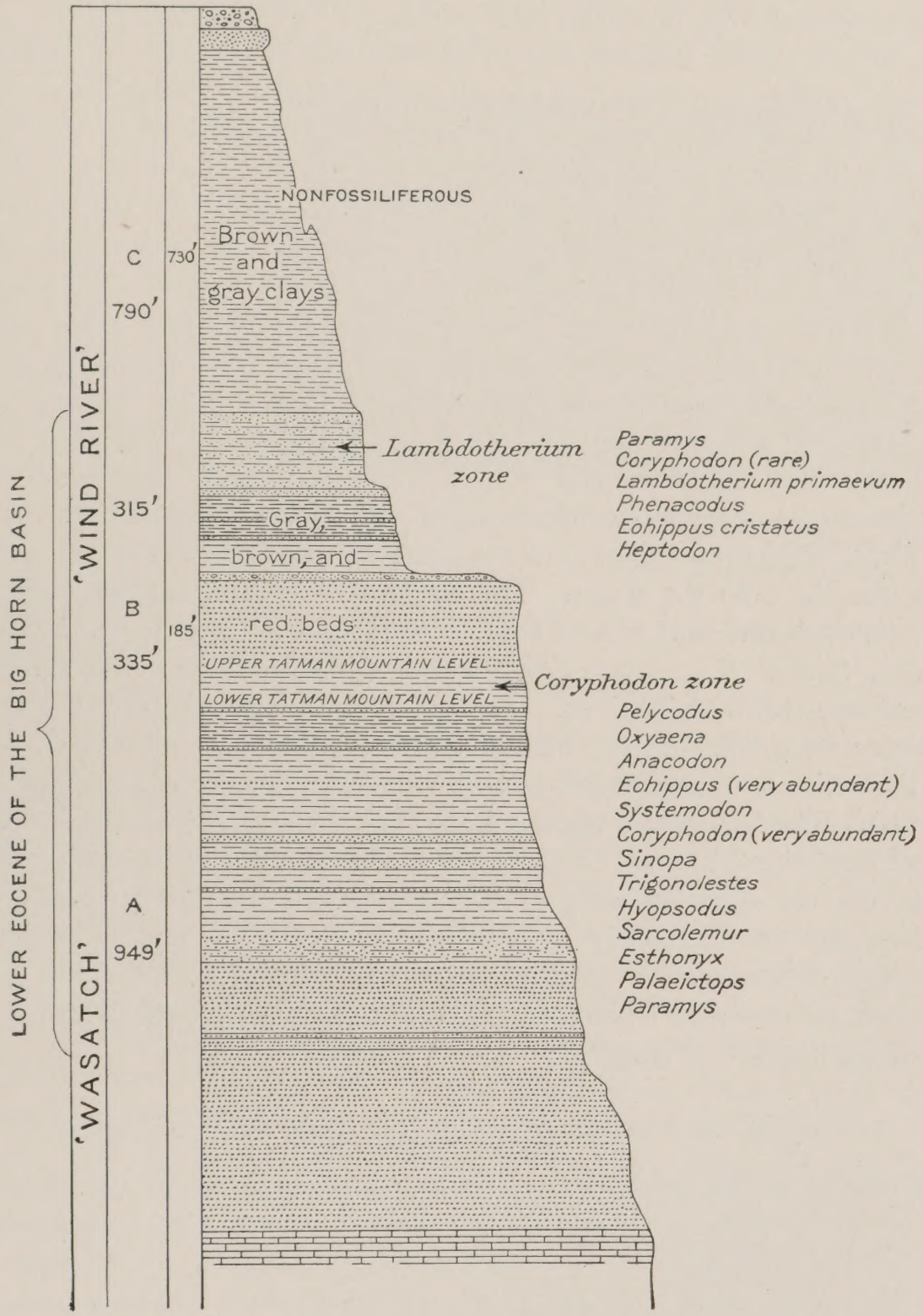


FIG. 38. — Composite columnar section of the Wasatch and Wind River formations of Big Horn basin, compiled from sections by F. B. Loomis. See section A, Fig. 35. Total thickness 2,391 feet.

Wyoming in Wasatch times. — A glance at Fig. 35 enables us to restore two of these great basins, the Wasatch lying south of parallel 42°

[1] Johannsen, Albert, Petrographic Report on Rocks Collected by Professor H. F. Osborn, *U.S. Geol. Surv.* In Ms.

and the Big Horn traversed by parallel 44°, east of the Wasatch and west of the Big Horn ranges respectively, both vast flood plain and lacustrine basins surrounded by low mountain ranges. It is significant that at Evanston in the Big Horn (Fig. 36) and in the Wind River (Fig. 38) the mammals are found chiefly in or near the so-called "Red Beds." These beds may be an indication of the prolonged exposure of these sediments to the air, or of erosion from the reddish rocks of the Trias. The basins were formerly considered great lake basins, but the river, flood plain, and lagoon theory now prevails. Loomis (1907) [1] carefully analyzed the entire mammalian fauna of the Coryphodon Zone with reference to its bearing on the physiographic conditions in these old mountain ranges. He shows that, judging by the apparent adaptations to various modes of life, the total known species of the vertebrate fauna are divided as follows: aerial 3 per cent, cursorial, terrestrial, and arboreal 75 per cent, amphibious 12 per cent, aquatic 10 per cent. We may imagine that this small percentage of species of truly aquatic animals, such as crocodiles, fishes, and turtles, mingled their remains with those of the prevailing land animals by becoming stranded or inclosed in lagoons far from the rivers. The bones of terrestrial animals may have been exposed on the sunny flats. The light-limbed horse *Eohippus*, probably typical of a plains or partly open country, alone makes up 32 per cent of the total collections. All the other perissodactyl or odd-toed ungulates were light-limbed, including the lophiodonts (*Heptodon*), primitive titanotheres (*Lambdotherium*), the surviving archaic condylarths (*Phenacodus*). The feet of all these animals indicate dry rather than swampy ground conditions, because they are more slender than those of the modern tapir. On the other hand, the coryphodons were certainly marshy-land dwellers, and perhaps partly amphibious, or stream dwellers, although this is far from demonstrated. The presence of rivers of considerable size is indicated by the large lepidostean fishes, or garpikes (*Clastes*), and by the river-living turtles (*Trionyx*).

Wasatch Life of the Wyoming and New Mexico Region

Surviving archaic mammals. — Taken altogether, the prevailing resemblances of this older fauna of the Coryphodon Zone are with the mammals found in the Sparnacian and Lower Ypresian of Europe, but far closer comparisons are necessary than any which have been made hitherto.

Of the smaller Herbivora, no signs of the Plagiaulacidæ or any other marsupials have been discovered; opossums (Didelphyidæ) were probably living in the forests of this region, however. Of the condylarth ungulates, *Phenacodus* is the most famous. The discovery by Wortman [2] of the

[1] Loomis, Origin of the Wasatch Deposits. *Amer. Jour. Sci.*, May, 1907, Ser. 4, Vol. XXIII, pp. 356–364.

[2] See Cope, E. D., The Vertebrata of the Tertiary Formations of the West. *Rept. U.S. Geol. Surv. Terr.*, Vol. III, 1883 (1884), Pl. LVII and text.

complete skeleton of *P. primævus* with its five digits on the fore and hind feet and its primitive bunodont teeth was welcomed as realizing the prototype or atavus of the Ungulata; but more profound study has revealed that this extremely small-brained (Fig. 40), long-tailed animal, replete with archaic unguiculate characters, is not the ancestor of a new and vigorous stock, but the survivor of a dying-out stock. Like its amblypod contemporaries, the Wind River species, *P. wortmani* was less abundant and of diminished size. A contemporary condylarth of the proportions of a modern hyrax is *Meniscotherium* (Fig. 39), with its very complex bunolopho-selenodont grinding teeth and reduced cropping teeth.

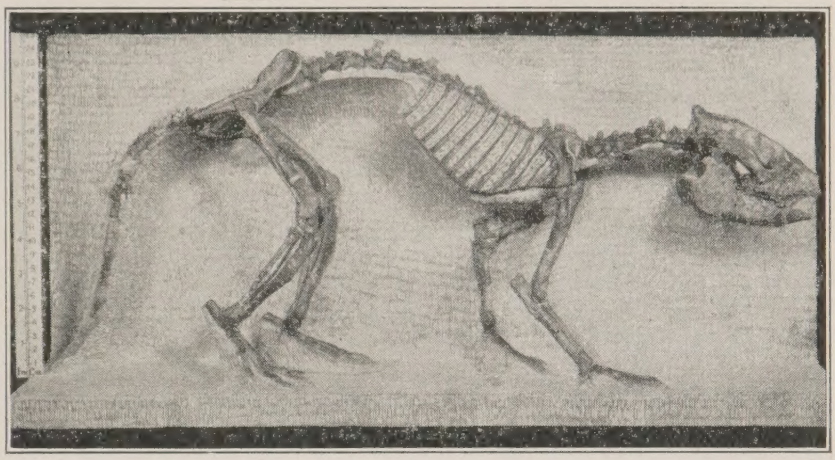


Fig. 39. — Skeleton of the Lower Eocene condylarth *Meniscotherium terræ rubræ*. In the American Museum of Natural History. (*N.B.* The scapula is only partially restored.)

The heavy-limbed Amblypoda of the period include several species of *Coryphodon*, attaining the proportions of small rhinoceroses, with crested grinding teeth and defensive canine tusks. These animals were termed Pantodonta by Cope, in reference to the complete series of upper and lower incisors. They have a rather feebly developed chest and musculature of the lumbar region, abbreviated tail, short, clumsy feet, and may have been partly amphibious in habit. The skull marks a great advance upon that of the ancestral *Pantolambda*, and rudiments of the posterior pair of osseous horns, characteristic of the succeeding genus *Uintatherium*, are observed.

A new order (Tillodontia) of gnawing diprotodont phytophagous placentals is heralded in species of *Esthonyx*, in which one pair of the incisor teeth is beginning to enlarge at the expense of the others, prophetic of the fully diprotodont *Tillotherium* of the Middle Eocene. The supposed aberrant Edentata of the order Tæniodonta, or Ganodonta, succeeding the Torrejon Stylinodontidæ, are now represented by the still more progressive *Calamodon*, with a deep-set pair of anterior teeth and still more reduced enamel on the grinding teeth. The tendency of these herbivorous forms to become diprotodont, or enlarge a pair of front teeth, is thus manifested independently in two orders. The Insectivora are now represented by three and perhaps four families, namely, the pantolestids (*Palæosinopa*), believed to be long-tailed aquatic forms analogous to the potamogalids of modern Africa; the leptictids (*Palæictops*), probably terrestrial forms of the size of the hedgehog (*Erinaceus*); the hyopsodontids (*Hyopsodus*), with teeth like those of *Eohippus* on a miniature scale, animals which were long regarded

as Lemuroidea, but are now transferred to the Insectivora on skeletal characters. There are other small forms (*Diacodon*, *Didelphodus*) which are of uncertain affinity. Preying upon these insectivorous and herbivorous forms are members of five families of the carnivorous Creodonta, including

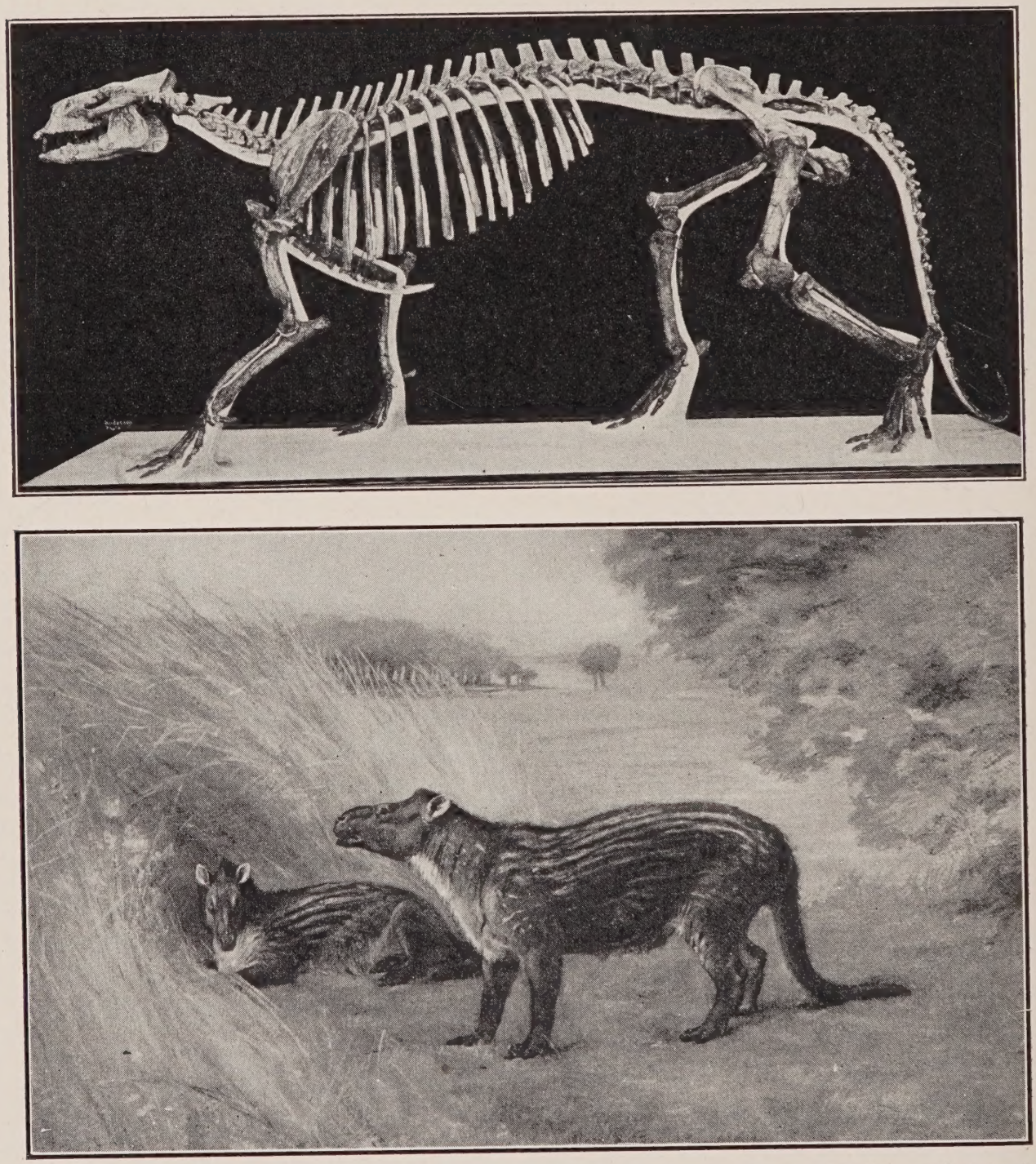


Fig. 40. — Lower Eocene light-limbed condylarths, or phenacodonts, showing arched back and long tail. Above : The skeleton of *Phenacodus primævus* (Cope's famous type). Below : Restoration by Charles R. Knight. Both in the American Museum of Natural History.

specialized Arctocyonidæ with flattened tubercular teeth (*Anacodon*), which make their last appearance. The giant carnivores or omnivores of the period are the mesonychids of the genus *Pachyæna*, descended from the Torrejon *Dissacus*, with blunt, rounded cusps adapted to devouring decaying flesh. In wide contrast are the palæonictids (or oxyænids) represented by *Palæ-*

onictis, of the size of a puma (*Felis concolor*), with sectorial teeth, short face and jaws. Another branch of oxyænids includes animals of smaller size (*Oxyæna*) with sharp and effective sectorials. Of the size of the modern civets (*Viverra*) are several species of *Sinopa*, adapted to the quest of birds and small mammals. Of great zoögeographic interest is the simultaneous distribution of three of these families (Palæonictidæ, Mesonychidæ, Hyænodontidæ) in the Lower Eocene of France.

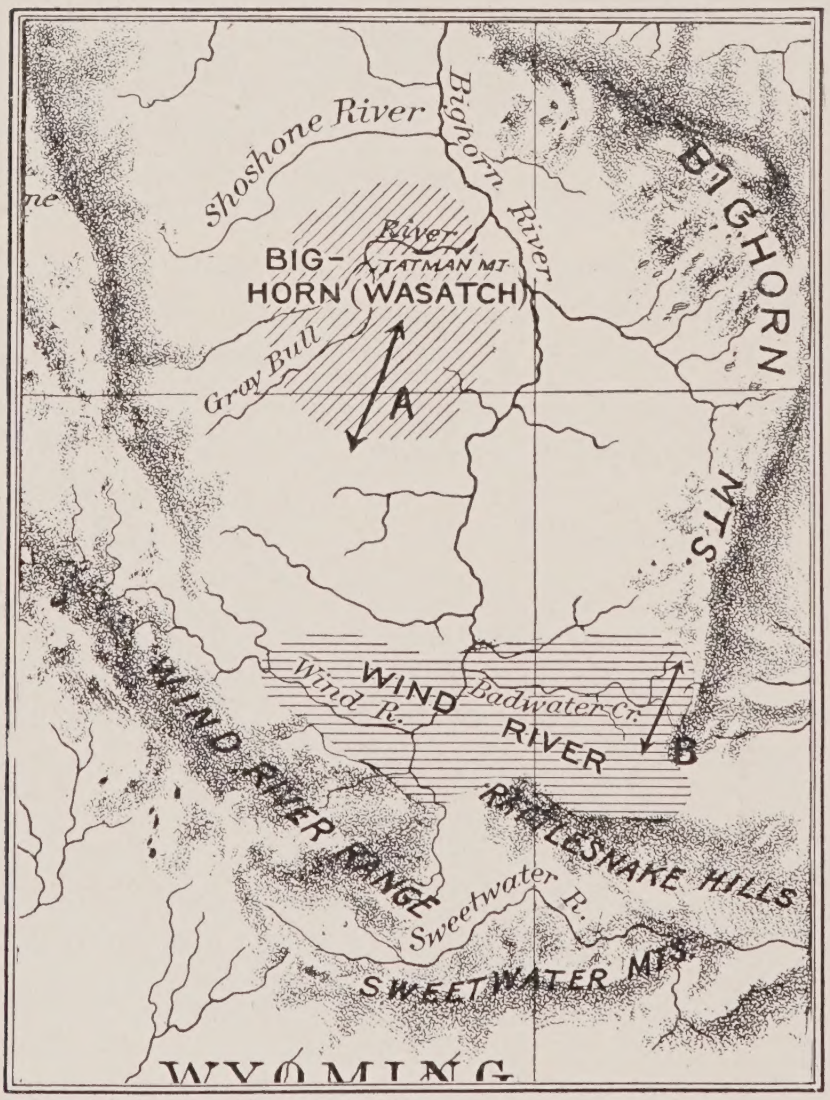
CHARACTERISTIC MAMMALS

Coryphodonts
Phenacodonts
Meniscotheres
Tillodonts
Tæniodonts
Insectivores
Arctocyonids
Mesonychids
Palæonictids
Oxyænids
Hyænodontids
Lemuroids
Rodents
Dichobunoids (Artiodactyls)
Lophiodonts
Hyracotheres

Progressive or modernized mammals.—Contrasting with these archaic, small, aberrant carnivores, are the members of the family Miacidæ, including *Didymictis*, surviving from the Torrejon, besides a great variety of small related carnivores (*Viverravus*, *Miacis*, *Uintacyon*, *Vulpavus*), all distinguished by the fact that the carnassial teeth are the same as those in the modern Carnivora, namely, the fourth upper premolar and first lower molar. Evidently these small true pro-carnivores were beginning to sharply compete for their prey with the small creodonts, although the larger creodonts (*Palæonictis*, *Pachyæna*) were alone capable of attacking animals of the size of *Coryphodon* and *Phenacodus*. The primates are now certainly recognized for the first time. Surprisingly modern is the Tarsius-like *Anaptomorphus*, a short-faced, large-eyed, aberrant form, with teeth analogous to those in the existing tarsier (*Tarsius*) of Madagascar, that is, not distinctly lemuroid. An insectivore of the diprotodont type or with an enlarged pair of lower front teeth is *Cynodontomys*, ancestral to the Microsyopidæ of the Bridger, and with some analogies to the Mixodectidæ of the Torrejon and the Plesiadapidæ of the Cernaysian. Among the herbivorous ungulates the greatest interest centers in the appearance of two families of even-toed or artiodactyl forms, the Trigonolestidæ, diminutive forms (*Trigonolestes*) with a typical artiodactyl astragalus, perhaps related to the Dichobunidæ (*Protodichobune*) of the Upper Ypresian. Of more doubtful affinity are the supposedly pig-like achænodonts, represented by *Parahyus*, quite an uncertain reference. Of equal moment is the sudden appearance of three families of Ungulata-Perissodactyla, namely, the horses (Equidæ), tapirs (Tapiridæ), lophiodonts (Lophiodontidæ). The lophiodonts are represented by the excessively slender-limbed and narrow-footed *Heptodon*, analogous in size only to the *Chasmotherium* of the Ypresian of France, but distinguished by dolichocephaly. Known in America only, at this stage, are the tapirs (*Systemodon*), animals somewhat exceeding the modern foxes (*Vulpes*) in size. Still more numerous and characteristic, as well as diversified, are the horses, including eleven species which have been discovered in the

different exposures of the Wasatch, all animals of the size of small foxes, graceful, light-limbed, and like their European contemporaries (*Hyracotherium*), large-brained. Close comparison (cf. p. 116) of these hyracotheres with those of the Lower Ypresian (London Clay) of the northern coast of Europe shows that the grinding teeth are in a very similar stage of evolution. The species *Eohippus validus*, on the whole the most ancient in type of the American hyracotheres, is in exactly the same state of evolution as the *H. vulpiceps* of the London Clay; but nothing in America is known quite so ancient as the *H. leporinum* of the London Clay in respect to the simplicity of the anterior premolar teeth.

A modern aspect is also given to this fauna by the appearance of the Rodentia (*Paramys, Sciuravus*) of the family Ischyromyidæ, embracing a number of species suggesting in their tooth structure the sciuromorphs, or squirrel group of rodents. It appears probable that some of these ischyromyids were destined to give rise to the true sciurids or squirrels.



By permission of the U.S. Geological Survey.

FIG. 41. — Map showing location of the Wasatch (oblique lines) and Wind River (horizontal lines) of the Big Horn region of Wyoming.

Wind River Life of Wyoming and Colorado

Geological conditions and distribution. — In their grand sequence the Wind River sediments and their geologic parallels in Wyoming and Colorado take up the life story of the Wasatch and continue it into the beginning of the Bridger deposition, which we regard as true Middle Eocene.

The typical formation lies at the head waters of the Big Horn River (Fig. 41), northeast of the Wind River Mountains, 400 to 500 feet in thickness, irregularly disposed with an east and west extent of 100 miles and north and south extent of forty miles.

It is readily distinguished geologically (Fig. 43) by horizontal alternating bands of gray and bright red fossil-bearing rocks. These red bands contain most of the fossils, and some are of considerable horizontal extent. The basin has been explored successively by Hayden (1859, 1869), by Wortman for Cope (1880) and the American Museum of Natural History (1891, 1896), by Loomis for Amherst College (1904), and by Granger (1905, 1909) for the American Museum. To the latter we are indebted for the first accurate survey of the geology and of the life succession in this basin as here set forth.[1] All previous accounts are incorrect, first, in attributing too great thickness to the Wind River deposits, second, in failure to connect them properly with the underlying Wasatch.

The sequence of the Wind River life zone to that of the Wasatch is clearly indicated in the Tatman Mountain section (Fig. 38) at the summit of the Big Horn Wasatch deposition (Fig. 41) to the north; here we clearly pass from the Wasatch into Wind River times.

While these formations were being deposited in Wyoming there was accumulating in southeastern Colorado the base of the Huerfano Formation, discovered by Hills[2] in 1888 and explored by Osborn[3] and Wortman in 1896. The basin lies immediately north of the famous twin volcanoes known as Spanish Peaks, and the Huerfano deposits are most probably tuffs, or of volcanic dust origin. The fossils apparently occur in a single stratum not exceeding ten or fifteen feet in thickness and not more than thirty or forty feet from the base of the formation. They include the remains of ten genera and of several species characteristic of the Wind River deposits. While the lower Huerfano levels are of Wind River age, the upper levels are distinctively of Middle Eocene, or Bridger age.

The Wind River life has thus been found in three chief localities:

Wind River of Wyoming, 500 feet.

Tatman Mountain, upper levels of 'Big Horn Wasatch' of Wyoming, 300 feet.

Huerfano of southeastern Colorado, 800 feet, including 'Bridger' levels.

Geographic conditions. — Loomis (1907) has rightly regarded the Wind River Formation as of fluviatile and flood plain origin. The wide horizontal extent of the red bands is attributable to prolonged or repeated periods of flooding; the red color is less probably due to aridity or other atmospheric causes than to erosion from the Triassic rocks. Besides a great variety of mammals, the 'red beds' contain turtles (*Trionyx*), crocodiles (*Crocodilus*), and lizards of the family of Anguidæ (*Glyptosaurus*). The

[1] See also forthcoming *Bull. Amer. Mus. Nat. Hist.*, by Walter Granger.

[2] Hills, R. C., Recently Discovered Tertiary Beds of the Huerfano Basin, Denver, 1888.

[3] Osborn, The Huerfano Lake Basin, Southern Colorado, and its Wind River and Bridger Fauna. *Bull. Amer. Mus. Nat. Hist.*, Vol. IX, 1897, pp. 247–258.

intermediate grayish 'shales,' as well as the coarse conglomerate beds formed by rapid stream action of river invasions, are barren.

Even in the 'red beds' fossils are scarce except in one or two very limited areas, and as a rule fragmentary and imperfectly preserved. The only complete skeleton recorded is the type of the famous *Eohippus venticolus*,

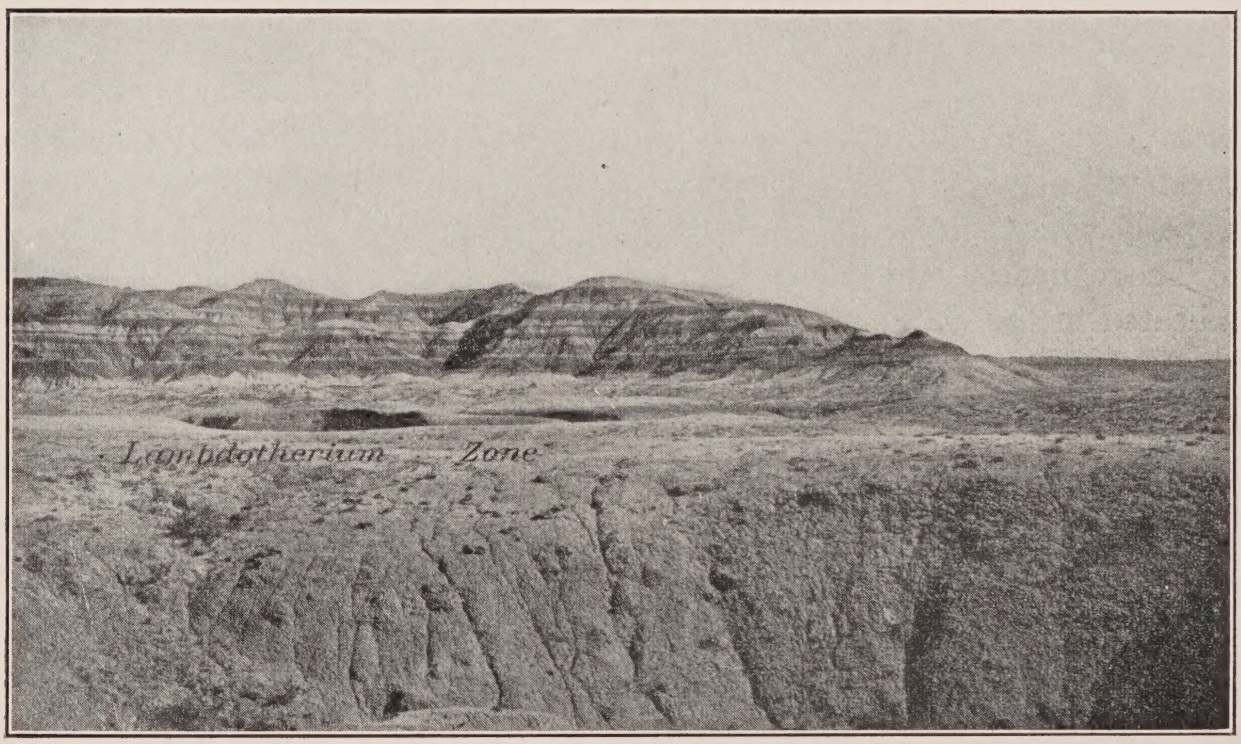


FIG. 42. — The Lower Eocene banded layers of the Wind River Badlands, basin of the Wind River, Wyo. Zone of *Lambdotherium* and of the last stages of *Coryphodon*. Photograph by American Museum of Natural History, 1896.

found by Wortman in 1880. It has required years of the most arduous search, concluding with the 'microscoping' of the beds by the American Museum party of 1909, to round out materials for our knowledge of this, including the discovery of the skulls of two of the most characteristic forms.

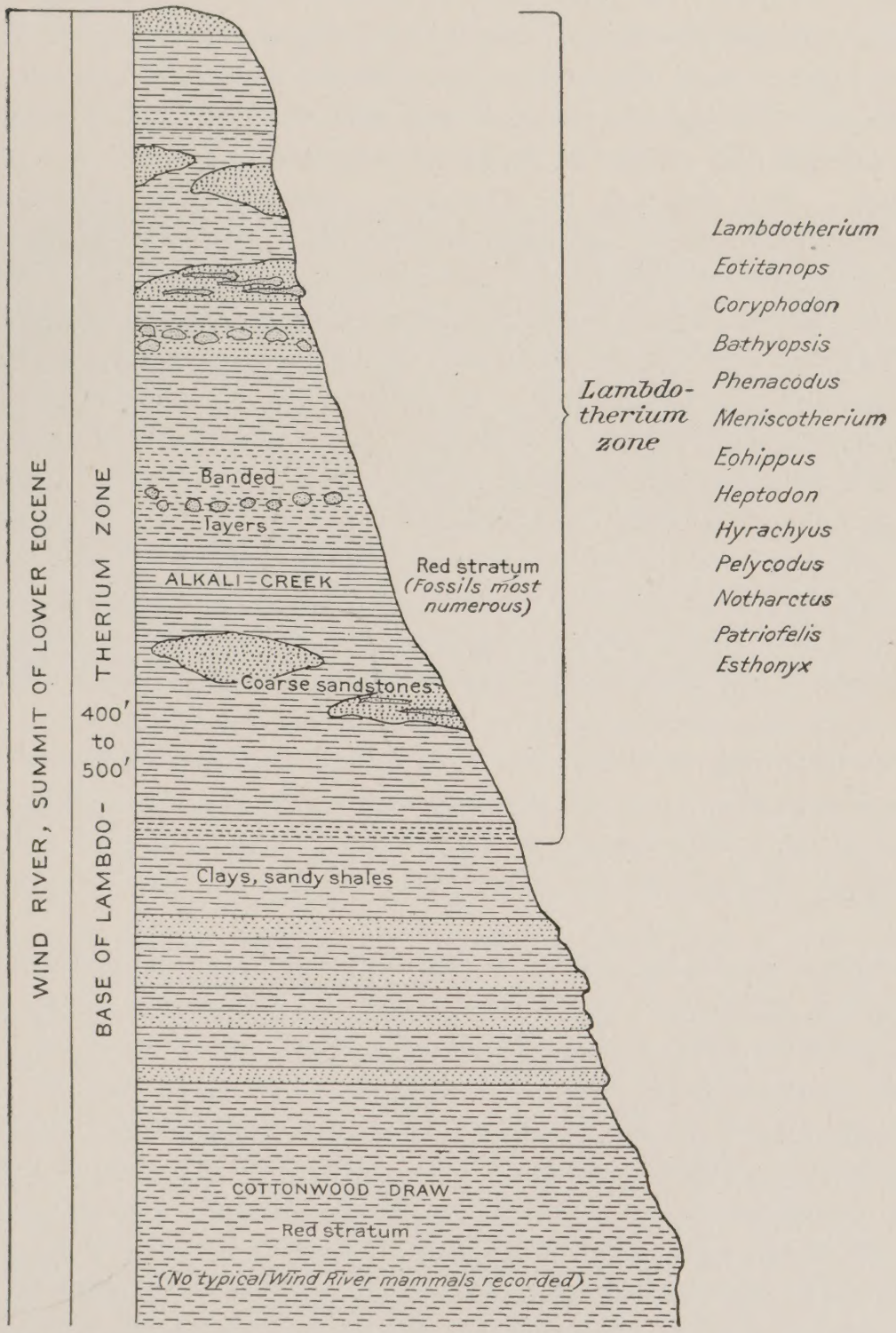
NEWLY ARRIVING MAMMALS

Titanotheres
Lambdotherium
Eotitanops
Hyracodonts
Hyrachyus
Uintatheres
Bathyopsis
Primates
Notharctus
Washakius
Microsyops

Faunal life. — With the Wind River we enter a new life zone, signalized by the earliest record of a new and very important family of perissodactyls, the titanotheres, which is represented by the genus *Lambdotherium* from which the zone takes its name. Accompanying this small, light-limbed and very abundant titanothere is the larger titanothere known as *Eotitanops*, a form truly ancestral to the great titanotheres of Eocene and Oligocene times. There are many other newly arriving mammals, including twelve new genera and fifty-five species, which have not been found in the Wasatch. Nine of these new genera of mammals are also found in the Bridger. Wind River life is thus transitional and prophetic of Bridger life. The Wind River, however, represents

Carnivores
Oödectes
Patriofelis
Limnocyon
Tritemnodon
Edentates
Stylinodon

truly the closing chapter of the Lower Eocene, because there is remarkably little extinction, there being rather a numerical diminution of the mammals so highly characteristic of the Lower Eocene. In all, the Wind River possesses twenty-five genera in common with the Wasatch. It possesses eleven Wasatch species. It is doubtful whether a single family of mammals becomes extinct.



By permission of the American Museum of Natural History.

FIG. 43.—Section of the Tertiary deposits of the Beaver Divide in the Wind River Basin, Wyoming. After Granger, 1910.

With the arrival of the new and retention of the old life, the Wind River stands directly intermediate in position; in fact the archaic and modernized mammals are nearly evenly balanced, as shown in the following summary:

Wind River Genera and Species

	Genera	*Species*
Archaic mammals	21	30
Modernized mammals	22	36

In this estimate, as before, the Insectivora are somewhat arbitrarily placed with the archaic, the Lemuroidea with the modernized forms. However reckoned, this balance between representatives of families destined to become extinct and those destined to populate the earth is extremely interesting. Two families of creodonts (Arctocyonidæ, Palæonictidæ) are sparingly represented, and have possibly disappeared. No other families or genera are known to have become extinct.

Archaic mammals. — The chief surviving archaic mammals are the coryphodonts, the condylarths, including *Phenacodus*, *Ectocion*, and *Meniscotherium*, three families of creodonts (Oxyænidæ, Hyænodontidæ, Mesonychidæ), the insectivores, the tillodonts, and the edentate tæniodonts. Among the archaic Ungulata it is noteworthy that both *Coryphodon* and *Phenacodus* are apparently diminished in number. It was supposed until recently that they were also dwindling in size, but this proves to be an error, because large forms of both animals were discovered by the American Museum party of 1909, including a phenacodont as large as the *P. primævus* of the Wasatch. Undoubtedly the competition between the condylarths and the smaller but better endowed horses, tapirs, titanotheres, and lophiodonts was becoming very severe. It is extraordinarily interesting to find the little *Meniscotherium* of the Wasatch again appearing in the Wind River. There are three or four species of *Coryphodon*, including chiefly animals of much smaller size than prevail in the Wasatch, and also one form of robust size.

Simultaneous with the decline of the coryphodonts, it is most interesting to record the appearance of the first member (*Bathyopsis*) of the related family (Uintatheriidæ) of giant Amblypoda which are destined to become the great quadrupeds of the Middle Eocene. For years only the jaw of the type species (*B. fissidens*) was known, but a skull discovered by Olsen of the American Museum party of 1909 shows that the animal possessed a pair of nasal frontal horns above the orbits, although there are no horns on the back of the skull, as in the Bridger successor, *Uintatherium*.

Of the diprotodont, gnawing, or leaf-eating mammals, the small Wasatch type (*Esthonyx*) persists, representing the order Tillodontia, which is also destined to survive into Bridger times. Among the tæniodonts, or supposed primitive Edentata, the large Wasatch type *Calamodon* survives and a

smaller, very progressive Bridger form *Stylinodon* first appears; this animal is distinguished by the long-crowned grinding teeth, beginning to grow from persistent pulps.

Little change appears among the Insectivora, since all the Wasatch families and genera survive or pass into more advanced mutations or stages. It is noteworthy that members of the supposed insectivore genus *Hyopsodus* attain a large size at this time and are the most abundant of Wind River mammals.

The opossums, or Marsupialia-Didelphyidæ, are possibly represented at this time in the species *Peratherium comstockii* recorded by Loomis, or in the problematic form *Didelphodus*.

Of the ancient Carnivora the Creodonta are now represented by three families: (1) the Mesonychidæ, including the giant *Pachyæna;* (2) the

FIG. 44. — The Lower Eocene creodont *Oxyæna* preying upon the carcass of *Eohippus*. After original by Charles R. Knight in the American Museum of Natural History.

Hyænodontidæ, which are still limited to two animals about the size of the fox, namely, *Sinopa*, the creodont most widespread geographically of any geologic period, and *Tritemnodon*, both animals possessing slender bodies and long and slender heads; (3) among the Oxyænidæ is one species of *Oxyæna* of intermediate size, and there first appear in this family at this time the primitive *Limnocyon* and the specialized short-faced *Pdtriofelis*. The latter animal is cat-like, large-limbed, nearly as large as the South American jaguar (*Felis uncia*), and becomes especially characteristic of Middle Eocene, or Bridger times. The bear-creodonts, or arctocyonids, are doubtfully represented in the Wind River and Huerfano depositions.

Progressive mammals. — The report by Cope of the existence of bats, or Cheiroptera, is an error; there are no certainly known bats in the entire American Tertiary. The supposed Middle Eocene (Bridger) bats reported by Marsh are talpoid insectivores.[1]

[1] Matthew, W. D., The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. *Mem. Amer. Mus. Nat. Hist.*, Vol. IX, Pt. 6, 1909.

The Rodentia are represented by the bunodont squirrel-like *Paramys*, surviving from the Wasatch, and the somewhat more rare *Sciuravus* of the primitive family Ischyromyidæ.

To be ranged among the ancient Creodonta or among the more modern pro-Carnivora is the family Miacidæ, which is now becoming highly diversified. It includes a variety of species which belong to the surviving Wasatch genera *Didymictis*, *Miacis*, and *Vulpavus*, as well as to the higher genera *Viverravus* and *Oödectes*. These animals are analogous in dental structure, in size, and in proportions to the civets and to the South American procyonids (*Bassariscus*, *Cercoleptes*) rather than to the dogs. The retention of the last lower molar is the only especial cynoid feature.

Similarly the Primates begin to take on a slightly more modernized form. There are the highly specialized *Tarsius*-like anaptomorphids, including two species, *Anaptomorphus spierianus* Cope, *A. abboti* Loomis, as well as a third representative of a new anaptomorphid genus. Related to the same family are diminutive monkeys allied to the *Omomys* and *Washakius* of the Bridger. We discover also the lemuroid or insectivoroid microsyopsids, including the Wasatch genus *Cynodontomys*, as well as the Bridger genus *Microsyops*. Similarly monkeys or lemurs of larger size represent the family Notharctidæ, which now includes not only the smaller Wasatch *Pelycodus*, but the more progressive *Notharctus*, a primate appearing here for the first time which becomes especially characteristic of the Bridger.

Of the cursorial Herbivora the odd-toed ungulates (Perissodactyla) are now enriched by the newly appearing family of Titanotheriidæ, both by the light-limbed *Lambdotherium* and the larger and more central *Eotitanops*. *Lambdotherium* is especially abundant, and characteristic of rocks of Wind River age wherever found. The prevailing species, *L. popoagicum* (named after a local stream, the Popoagie River), is an animal of the size of a coyote (*Canis latrans*), with a slender, elongate muzzle, and laterally compressed digits which suggest those of the contemporary equines; it was evidently a cursorial, or slender-footed form adapted to the open basins of the mountain region. The larger Wind River titanothere (*Eotitanops borealis*) is now about the size of a two-thirds grown tapir, and appears to possess all the characters which justify our regarding it as ancestral to certain of the Bridger and Upper Eocene titanotheres; whereas *Lambdotherium* belongs to a dying-out phylum. It is noteworthy that these members of the titanothere family, which is destined to become the dominant perissodactyl family of the remainder of the Eocene, are already dominant in size among the modernized herbivores of Wind River times, although inferior to the coryphodonts and uintatheres.

The horses are represented by the persisting Wasatch genus *Eohippus*, in which the hind feet retain the vestigial fifth digit, and there is little advance in the complication of the grinding teeth. The famous skeleton of *Eohippus venticolus*, discovered by Wortman and fully described and figured

by Cope (1884), is distinguished by its relatively elongate head, very slender limbs and digits, and the marked simplicity of its grinding teeth. The horse of the Huerfano country appears (Cockerell) to correspond with this

FIG. 45. — The Wind River Eocene four-toed horse, or *Eohippus*. As a forest-living form the animal is represented as spotted. The indication of a short mane is entirely conjectural. After original by Charles R. Knight in the American Museum of Natural History.

species both in its measurements and in the simple character of the crowns of its grinding teeth.

The lophiodonts are still represented by the Wasatch *Heptodon*, a slender-limbed animal.

Tapirs have not yet been discovered, but they undoubtedly existed at this time.

The family of hyracodonts makes its first appearance here, its presence being indicated by a single specimen of the genus *Hyrachyus*.

Fishes of the Green River Shales and Other Eocene Formations[1]

While the terrestrial life of the close of the Lower Eocene is so well portrayed in the Wind River Formation, the fluviatile, lacustrine, and plant life is equally well known through the shale deposits in the Green River Lake to the south (Fig. 35).

[1] Cope, E. D., The Vertebrata of the Tertiary Formations of the West. *Rept. U.S. Geol. Surv. Terr.*, Vol. III, 1883 (1884).

General. — The Eocene fishes of the Rocky Mountain region are partly known in the Wasatch (Lower) and Bridger (Middle), and far more fully in the intermediate *Green River Shales*, which, since they are found to lie intermediate between the Wasatch and Upper Bridger, are considered of the same age as the Wind River and the Lower Bridger formations. The fact of most general interest is that the fishes are partly those of the existing freshwaters of the interior of the United States, and partly those now characteristic of South America, Australia, and Africa. Thus in the Bridger we find the Lepidosteidæ represented by the garpike (*L. anax*), as large as the largest alligator gars of the Mississippi. In this formation, as well as in the Bridger and Washakie, the other American ganoid family of bowfins (Amiidæ) is abundantly represented. The siluroid, or catfish, order Nematognathi, represented in the Bridger and Washakie *Rhineastes*, is now widely distributed in South America. This South American distribution is more clearly represented in the remarkable deposits of the Green River.

The Green River Lake Formation. — From the evidence afforded by the fishes, the Green River Shales are best explainable as either an estuarine or a land-locked bay deposit. On such a supposition only can we account for the preponderance of river forms with a small admixture of marine or coast forms, such as *Notogoneus*, belonging to a family (Gonorhynchidæ), the living members of which are all strictly marine (Cope, Smith Woodward), or the sting ray, *Dasyatis*, a member of the order of sharks, allied to existing forms which frequent the streams and estuaries of Florida as well as the adjacent coasts (Boulenger). Altogether the fishes represent three major groups: elasmobranchs (sting rays), ganoids (*Lepidosteus*, *Amia*), and teleosts. A large part of the teleosts are related to fishes at present confined to the southern hemisphere. Thus the diplomystids ('rough-backed herrings') survive only in certain rivers and along portions of the coasts of Chili and eastern Australia; *Dapedoglossus* or *Phareodus* and *Priscacara* belong to families now chiefly distributed in South America, Africa, and Australia.

These Neotropical and possibly Antarctic affinities coincide with those displayed in the turtles and tortoises described below (see Bridger Basin).

The fishes thus indicate, first, that the Green River Lake still preserved or had only recently lost connection with the sea, and second, that western North America had enjoyed long-continued continental connection with western South America. They may also be interpreted as favoring the highly improbable 'Atlantis' hypothesis.

The flora [1] also presents some indications of South American affinity in *Manicaria*, a palm now confined to Guiana, and in *Zizyphus*, a tropical plant. Here also we find the palms *Sabal* and *Flabellaria*, horsetails (*Equisetum*), and among the ferns the genus *Acrostichum*, which is now confined to the

[1] Newberry, J. S., and Hollick, A., The Later Extinct Floras of North America (edit. by Hollick). *U.S. Geol. Surv.*, Vol. XXXV, 1898.

West Indies and New South Wales. The sequoias are represented by *Nordenskioldia*. Among the northern trees are willows, oaks, and planer trees (*Planera*).

III. MIDDLE AND UPPER EOCENE LIFE OF EUROPE AND AMERICA

Near the close of the Lower Eocene the interchanges of mammalian life between the New and Old Worlds apparently ceased, and the mammals of the two great holarctic colonies entered upon a long period of independent and partly divergent evolution which lasted until the summit of the Eocene,

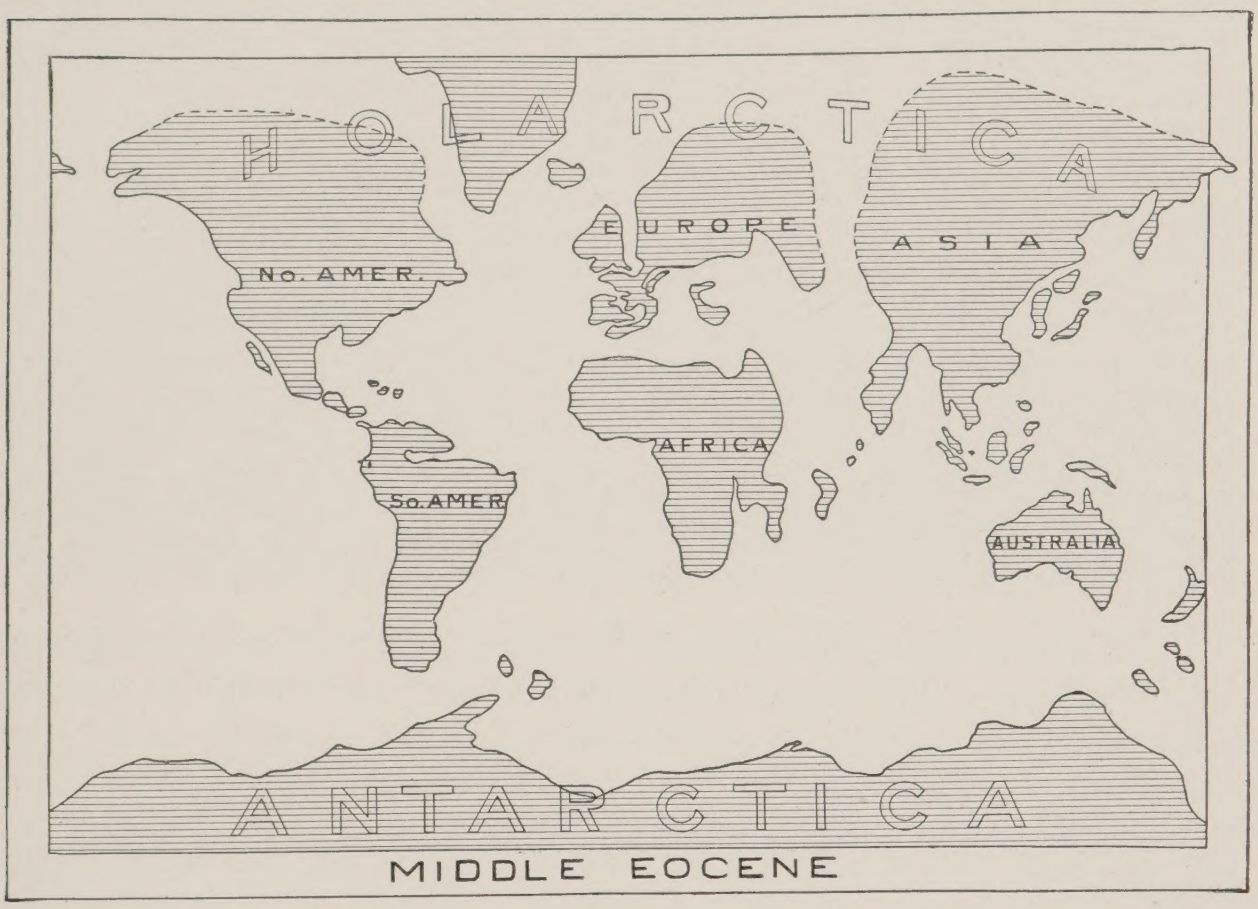


FIG. 46. — **Middle Eocene.** A period of continental depression, or geographic isolation of the New and Old World mammals, resulting in prolonged independent evolution and adaptive radiation on the great continents. Australia probably separated. The archaic and modern mammals giving rise to independent groups of mammals in (1) North America, (2) Eurasia, (3) North Africa, (4) South America. Rearranged after W. D. Matthew, 1908.

as first pointed out by the writer in 1899 [1] and subsequently emphasized by Stehlin [2] and Matthew.[3] Whereas in the Lower Eocene, owing to a continuance of the Basal Eocene community of life and to the invasion of similar modernized families, the two continents, that is, western Europe and the Rocky Mountain region, were united by the presence of nine families and

[1] Osborn, H. F., Tertiary Mammal Horizons of Europe and America, 1899–1900, p. 7 fol.

[2] Stehlin, H. G., Sur les Mammifères des Sables Bartoniens du Castrais. *Bull. Soc. Géol. France*, Ser. 4, Vol. IV, May, 1904, p. 473.

[3] Matthew, W. D., Hypothetical Outlines of the Continents in Tertiary Times (p. 361). *Bull. Amer. Mus. Nat. Hist.*, Vol. XXII, Art. xxi, Oct., 1906.

many genera of mammals, a faunal community which will probably be enriched rather than diminished by future discoveries in France, we now enter a long period of disunion. This disunion culminates in there being at the close of the Eocene only five families of mammals common to western Europe and the Rocky Mountains, namely, Lophiodontidæ, Dichobunidæ, Homacodontidæ, Equidæ, Hyænodontidæ, while at the same time eleven families of mammals are known in Europe which have not been discovered in America, and thirteen families are known in America which have not been discovered in Europe. We can thus hardly avoid the conclusion that there was a prolonged period of geographic or climatic isolation between the two regions, constituting a very distinct faunal phase, as follows:

III. THIRD FAUNAL PHASE — GRADUAL DIVERGENCE BETWEEN MAMMALS OF NORTH AMERICA AND THOSE OF WESTERN EUROPE, AND LITTLE EVIDENCE OF FAUNAL INTERCHANGE. NO EVIDENCE OF FURTHER NORTHERN OR EURASIATIC MIGRATION IN NORTH AMERICA. DESCENDANTS OF THE ARCHAIC AND MODERNIZED MAMMALS SLOWLY EVOLVING AND COMPETING WITH ONE ANOTHER DURING THE LOWER AND MIDDLE EOCENE. GRADUAL ELIMINATION OF THE ARCHAIC MAMMALS. CONTINUATION IN NORTH AMERICA OF SIMILAR CONDITIONS OF ENVIRONMENT.

As to life in the mountain region, attention may be especially directed to the evidence of uniform and favorable environmental conditions and persistent evolution throughout the Middle and Upper Eocene periods. The changes are those of progressive modification and adaptation rather than of breaks in the balance of nature by migration or extinction. Both the archaic and the modernized mammals increase in size and in variety. The changes are, moreover, specific rather than generic. At the close of the Lower Eocene, or Coryphodon Zone, just considered, we have observed the elimination of the phenacodonts, coryphodonts, palæonictids, arctocyonids; no further very striking elimination occurs. The surviving archaic mammals appear to flourish and increase, especially in size and muscular power.

It is noteworthy that in this long period, and even up to the summit of the American Eocene, only three new or previously unknown families of mammals make their appearance. These are the ancestral camels (Camelidæ), the oreodonts (Oreodontidæ), and the primitive armadillos (Edentata Dasypoda). In western Europe there is by contrast the repeated appearance of new families from some easterly and northerly sources.

Correlation. — Both in Europe and in North America a rich mammalian fauna opens the Middle Eocene and pursues a quite independent evolution in the Old and New Worlds during the entire Middle and Upper

Eocene which renders time correlation very difficult. There are some interesting contrasts similar to those which generally distinguish a peninsular from a continental fauna. The archaic herbivores (Amblypoda), which form the most striking feature of the Rocky Mountain fauna, are

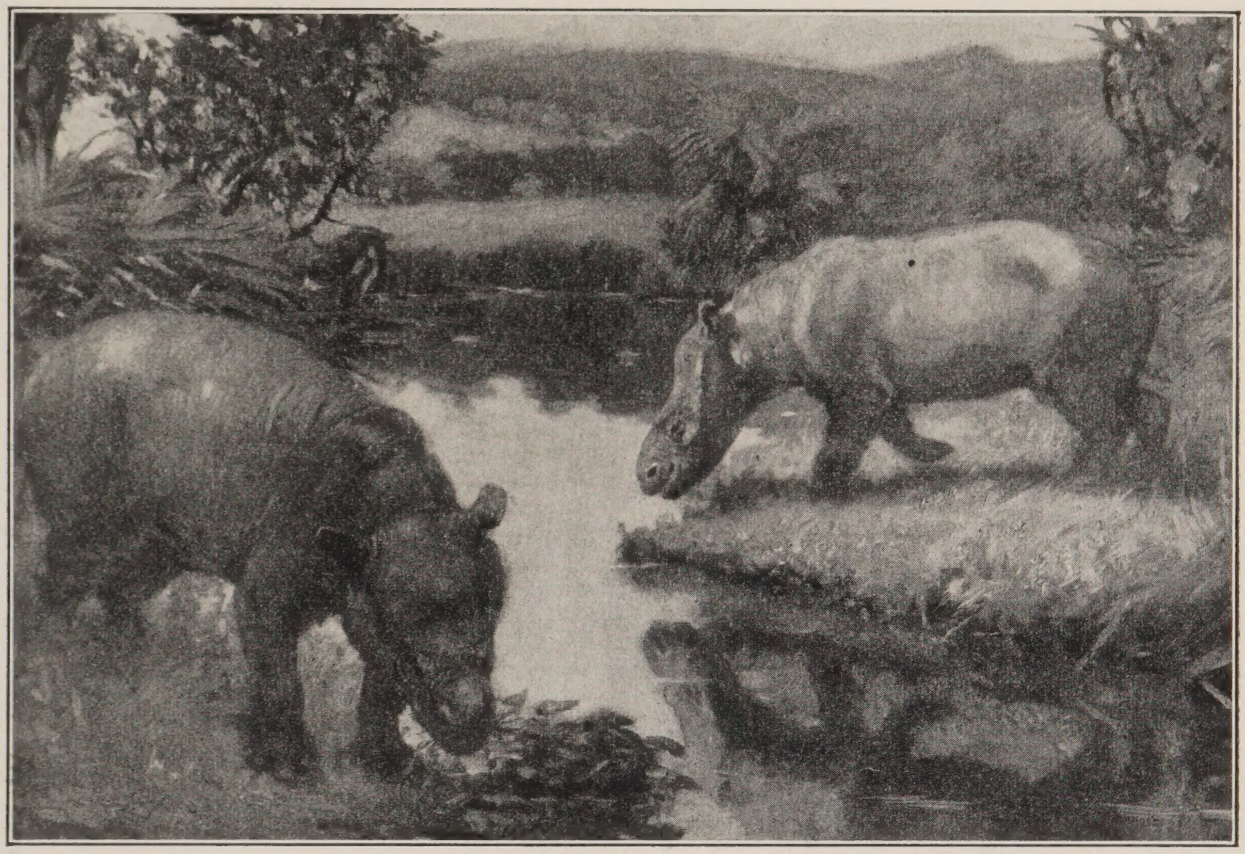


FIG. 47. — Divergence of Europe and America. Upper Eocene titanotheres, found only in North America. To the left the broad-skulled *Manteoceras;* to the right the long-skulled *Dolichorhinus*. After original by Charles R. Knight in the American Museum of Natural History.

entirely unrepresented and probably extinct in Europe. The archaic carnivores, which are represented by three powerful family types in the Rocky Mountains (*Mesonyx, Patriofelis, Sinopa*), embrace only a single family (Hyænodontidæ) in Europe. Altogether the North American fauna is much more diversified and more *continental* and cosmopolitan than the European. The European stages and their American parallels may be approximately correlated as follows:

	American Formations	*American Life Zones*	*Approximate European Stage*
UPPER EOCENE	Upper Uinta	Diplacodon Zone	LUDIAN
	Middle Uinta	Eobasileus Zone	LUDIAN
	Upper Washakie	Eobasileus Zone	LUDIAN
MIDDLE EOCENE	Lower Uinta	Uintatherium Zone	BARTONIAN
	Lower Washakie	Uintatherium Zone	BARTONIAN
	Upper Bridger	Uintatherium Zone	BARTONIAN
	Lower Bridger	Orohippus Zone	LUTETIAN
	Upper Huerfano	Orohippus Zone	LUTETIAN

Middle and Upper Eocene Life of Europe

Palæogeography.[1] — Early in the Lutetian the sea advanced southward around Paris and then proceeded to form the *calcaire grossier supérieur*, a fluviatile formation which gathered in remains of many ungulates. At the same time there were lake deposits at Argenton (1), a fissure deposit also rich in mammals, and at Lissieu (2) near Lyons. When the upheaval of the Pyrenees began, the climate became warmer. In France we have

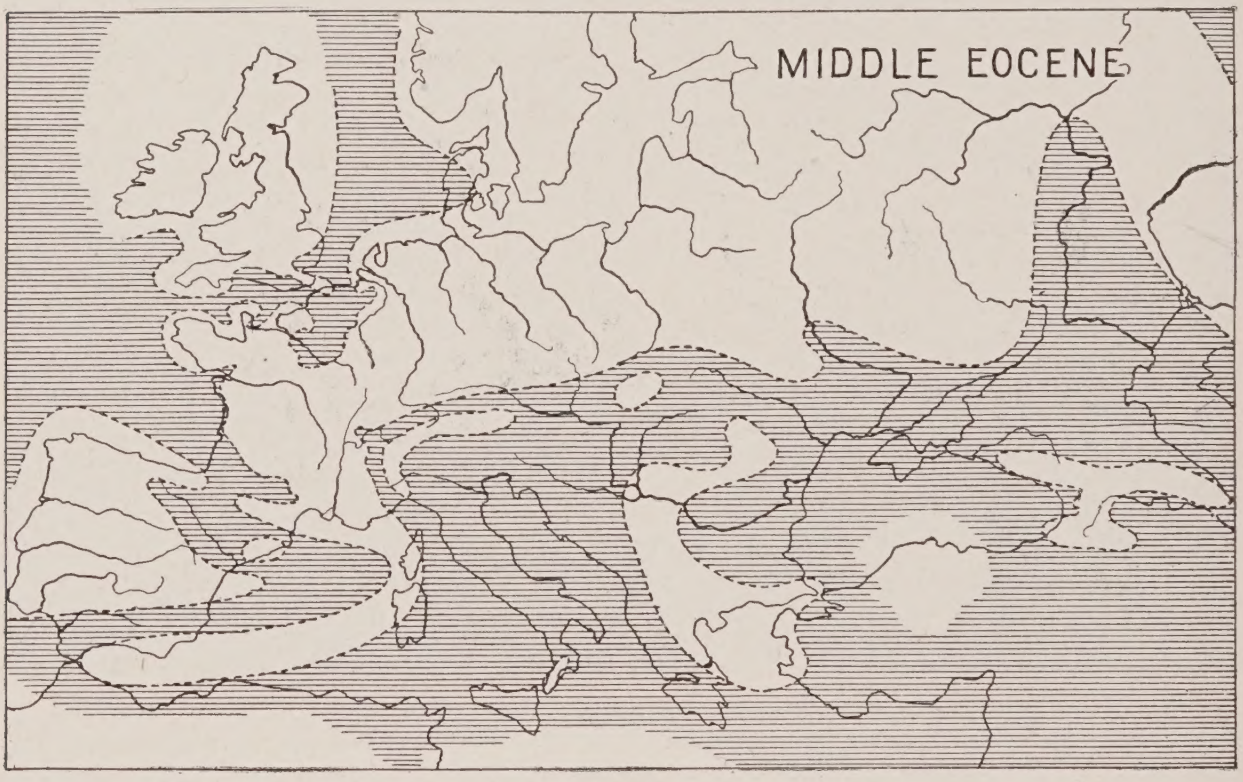


Fig. 48. — Europe in Middle Eocene, or Lutetian times. White = land. Ruled = sea. After de Lapparent, 1906.

evidence of a flora bearing an African aspect and including oleanders (*Nerium*). Palms flourished in southern England, and there were water gavials (*Gavialis*), crocodiles, and giant sea-snakes (*Palæophis*). The flora of Bournemouth suggests a comparison of climate with that of the Malay Archipelago and tropical America.

Our knowledge of the geographical distribution of the mammals rapidly widens, chiefly through the discovery of freshwater and fissure formations all over France and in southern England.

In the succeeding Bartonian stage there was a fresh marine invasion in the Paris Basin. In the southwest the sea receded as the upheaval of the Pyrenees continued, and in the Paris Basin lagoons began to form. The flora indicates that the climate remained warm as in the Lutetian stage; it includes palms (*Sabalites*, *Flabellaria*), laurels (*Laurus*), and *Podocarpus*, a conifer now confined to eastern Asia.

The Upper Eocene or Ludian stage marks the elevation of northern

[1] Cf. de Lapparent, A., Traité de Géologie, 1906, p. 1513 fol.

France and the consequent recession of the old Northern, or Suessonian Gulf, replaced in the Basin of Paris by a period of great lagoons, the evaporation of which caused thick deposits of gypsum. At the same time numerous small freshwater lake, river, and swamp deposits (lignites) collected mammal remains over a very wide area, reaching northern Spain, southern England, and Bavaria (Heidenheim) in the east, and giving us probably a very true picture of the entire fauna of western Europe. The lagoons were fed by freshwater streams, which brought with them remains of animals from neighboring districts. Those of the Paris *gypse* probably communicated with the sea by river channels to the north. The bed of the ancient lake of Velay contains a flora of African type, including the sabal (*Sabalites*) and the date palms (*Phœnicites*).

The Mammalian group as compared with that of America.—We first note in the Old World the entire absence of tapirs (Tapiridæ), of titanotheres (Titanotheriidæ), and rarity of pro-Carnivora (Miacidæ), as well as of many other archaic and modern forms of mammals which have been discovered in the American Eocene. The number of European Middle and Upper Eocene families surviving, or having descendants at the present day, is, in fact, very small, including only the horses (Equidæ), moles (Talpidæ), hedgehogs (Erinaceidæ), and possibly the aye-ayes (Cheiromyidæ). Possibly certain of the Old World dichobunes (Dichobunidæ) are ancestral to the modern ruminants. With these exceptions this is truly an ancient fauna, and so it impressed all the early French writers. It is not, however, an archaic fauna in the sense of being a survival from the Age of Reptiles, because the only archaic mammals are the hyænodonts and insectivores. This group represents, therefore, the first adaptive radiation of the higher kinds of placental Herbivora, radiating mostly into *browsing* types, which exhibit a great range of size and speed, and indicate a general prevalence of forested conditions and soft herbage. Without exception the grinding teeth are short-crowned or brachyodont. No distinctively grazing or hypsodont animals are known in all this assemblage. Stehlin [1] (1904, p. 473) observes: "Thus the aspect of the European fauna during the second half of the Eocene tends to become ever more homogeneous as our knowledge of it increases. It is a period of comparative calm, during which a number of types (lophiodonts) dominant at first, become extinct, while others (palæotheres) gradually gain in importance."

Like the mammals which appeared in North America late in Wind River and early Bridger times, this faunal group was destined to monopolize the European world during the Middle and Upper Eocene. The first extinctions occurred in the Bartonian. The first invasion of any considerable number of new mammals appeared at the very close of the Eocene or Ludian (see p. 145).

[1] Stehlin, H. G., Sur les Mammifères des Sables Bartoniens du Castrais. *Bull. Soc. Géol. France*, Ser. 4, Vol. IV, May, 1904, pp. 445–475.

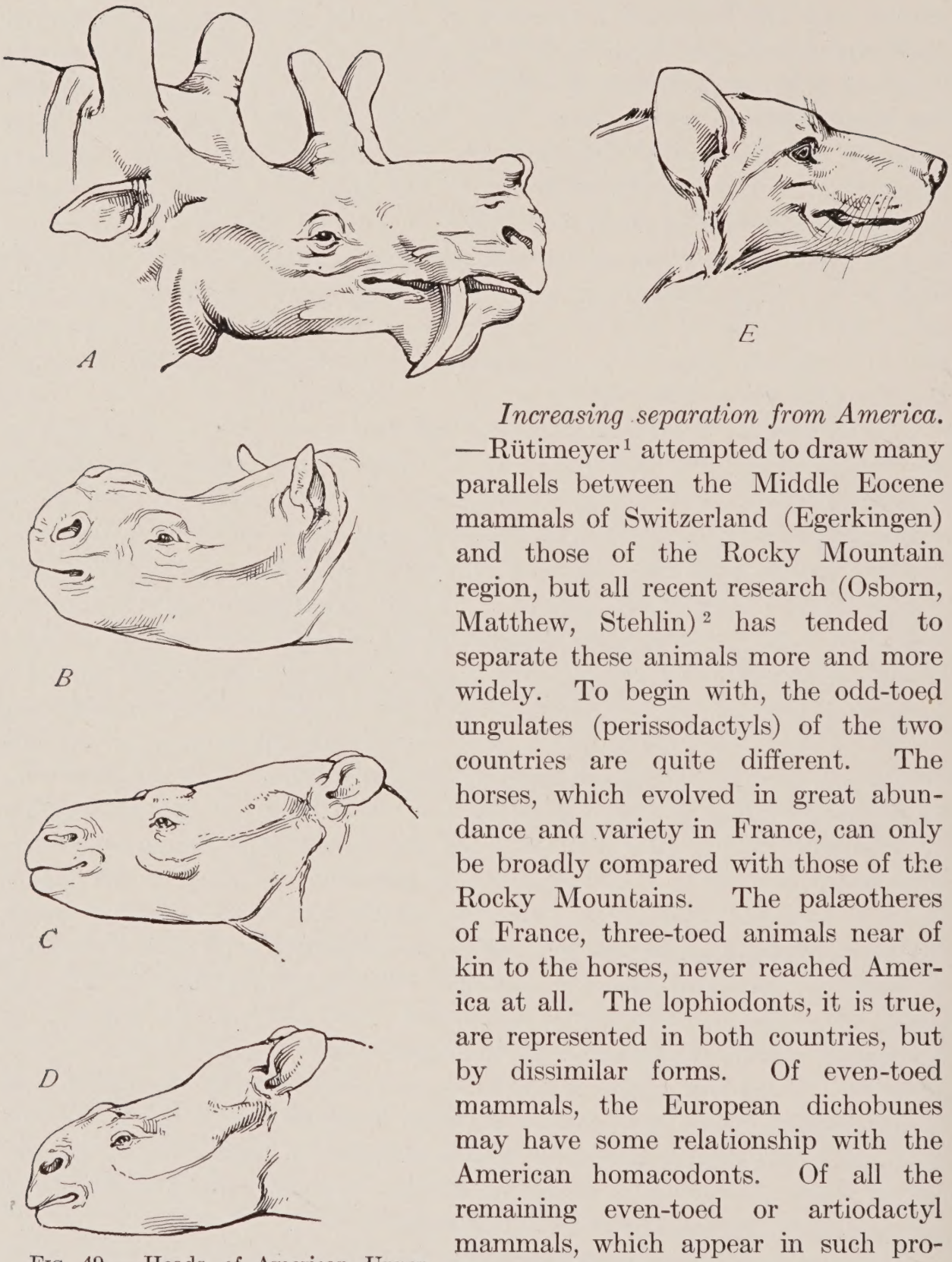


FIG. 49. — Heads of American Upper Eocene mammals not thus far known in western Europe.* Outline restorations by Charles R. Knight. *A. Eobasileus*, an amblypod. *B. Protitanotherium*, a titanothere. *C. Dolichorhinus*, a titanothere. *D. Manteoceras*, a titanothere. *E. Harpagolestes*, a creodont. Chiefly of Upper Washakie Age, Eobasileus Zone.

* It is possible that the family of titanotheres may have existed in eastern Europe at this time.

Increasing separation from America. — Rütimeyer[1] attempted to draw many parallels between the Middle Eocene mammals of Switzerland (Egerkingen) and those of the Rocky Mountain region, but all recent research (Osborn, Matthew, Stehlin)[2] has tended to separate these animals more and more widely. To begin with, the odd-toed ungulates (perissodactyls) of the two countries are quite different. The horses, which evolved in great abundance and variety in France, can only be broadly compared with those of the Rocky Mountains. The palæotheres of France, three-toed animals near of kin to the horses, never reached America at all. The lophiodonts, it is true, are represented in both countries, but by dissimilar forms. Of even-toed mammals, the European dichobunes may have some relationship with the American homacodonts. Of all the remaining even-toed or artiodactyl mammals, which appear in such profusion in France, no counterparts whatever are found in America. This is true as well of the carnivores and other unguiculates; the so-called *Calamodon*,

[1] Rütimeyer, Die Eocäne Säugethier-Welt von Egerkingen. *Abhandl. schweiz. paläont. Gesell.*, Vol. XVIII, Zürich, 1861.

[2] See Bibliography.

supposed by Rütimeyer to be related to the tæniodont edentates of America, is now regarded by Stehlin as related to the aye-aye (*Cheiromys*) of Madagascar. The rodents also (*Plesiarctomys*) are remotely related,[1] as well as the primates, or lemuroids. The most American type of animal in the European Middle Eocene is perhaps the little carnivorous creodont *Sinopa* of Egerkingen, a representative of the family Hyænodontidæ, and, so far as known, somewhat like its Bridger contemporary. *Sinopa*, however, is a survivor of an old phylum; it is an alert and widespread animal distributed from the Rocky Mountain region to northern Africa.

The affinity, therefore, between America and Europe is only that of descent from similar ancestors; for the time Europe constitutes part of an entirely different zoölogical region, or *Palæarctica*.

Geological Succession

1. *Lutetian Stage.* — This initial stage (which takes its name from Lutetia, Paris), according to Depéret [2] exhibits (I) an older fauna of Argenton and Bracklesham, and (II) a newer fauna of the *calcaire grossier* of Paris. In the latter begins the *Palæotherium Zone*.

The older fauna marks the beginning of the fissure deposits of Lissieu (2) near Lyons and of Egerkingen (10), Canton Vaud, in Switzerland. The last, rich in the teeth of mammals, has been made famous through the researches of Rütimeyer,[3] who assigned them great geological antiquity. His successor, Stehlin, has properly placed them in the lower portion of the Middle Eocene.[4]

To the newer stage belong the rich deposits of La Levinière (Hérault) (7) recently explored by Depéret, yielding perfectly preserved skulls of lophiodonts and horses.

2. The succeeding *Bartonian Stage* receives its name from the Barton clays of Hampshire, England. It is sharply defined zoölogically as the close of the Lophiodon Zone, including the large final stage of lophiodont evolution (*L. lautricense*), in which the premolar teeth are complicated, whereas in the *L. rhinocerodes* of Egerkingen they are simple. With the disappearance of these dominant mammals Europe was left during the remainder of the Eocene without any quadrupeds larger than tapirs. The lophiodon *Chasmotherium* also disappears. The supposed chalicothere *Pernatherium*, a very aberrant perissodactyl, is first known at this stage. The mammals are otherwise a continuation of those of the Lutetian. Of the same age are

[1] *Plesiarctomys* is probably but not certainly closely related to or identical with *Paramys*. W. D. M.

[2] Depéret, C., L'évolution des Mammifères tertiaires (Eocène). *C. R. Acad. Sci. Paris*, Vol. CXLI, 1905.

[3] Rütimeyer, L., Die Eocäne Säugethier-Welt von Egerkingen. *Abhandl. schweiz. paläont. Ges.*, Vol. XVIII, Zürich, 1891.

[4] Stehlin, H. G., Die Säugetiere des schweizerischen Eocäns, Critischer Catalog der Materialien, III Teil. *Abhandl. schweiz. paläontol. Ges.*, Vol. XXXII, Zürich, 1906, pp. 593–595.

the lacustrine deposits of St. Ouen (12) near Paris. Fissure deposits or '*terrains sidérolithiques*,' analogous to those of Egerkingen and Lissieu, are represented in Heidenheim (Bavaria) (20) and Mormont near Lyons. Depéret considers the beginning of the famous fissures of Quercy (19) as

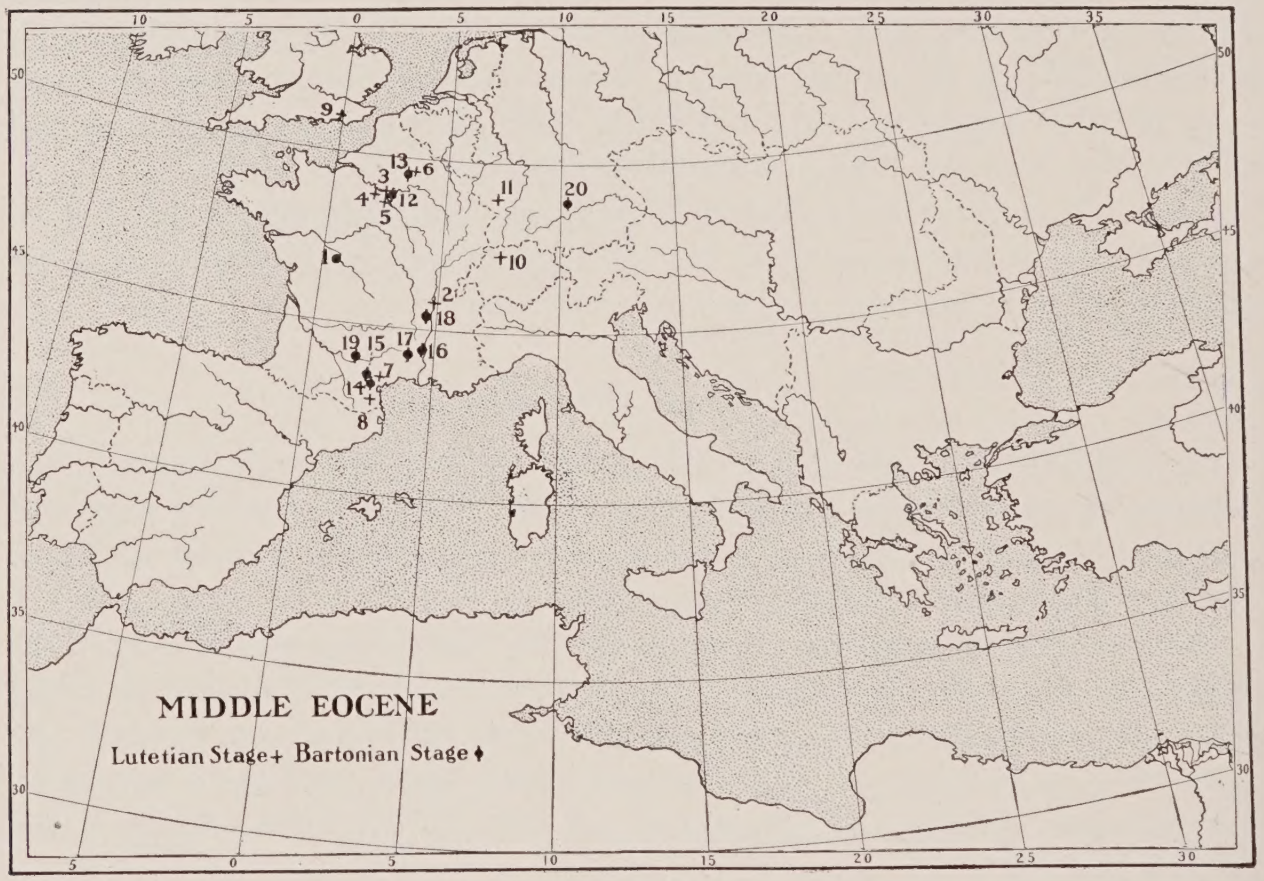


FIG. 50. — **Middle Eocene.** Lutetian. FRANCE. — Marnes d' **1** *Argenton* (Indre), lacustrine. Sidérolithique de **2** *Lissieu*, near Lyons, fissure deposits. Calcaire grossier de **3** *Paris, Vaugirard*, **4** *Nanterre*, **5** *Gentilly*, near Paris, lower strata marine, upper freshwater or brackish. **6** *Coucy, Dampleix* (Aisne). **7** *Les Matelles, La Levinière*, conglomérats et grès de *St. Gely du Tesc* (Hérault). Grès d' **8** *Issel, Cesseras*, in the Mts. Corbières. ENGLAND. — Series of clays, marls, sands, and lignites of **9** *Bracklesham* (Sussex), marine (100 ft.). SWITZERLAND. — Mergeln von **10** *Egerkingen*, in the Jura Mts., terrain sidérolithique. GERMANY. — Süsswasserkalk von **11** *Buchsweiler* (Alsace). Bartonian. FRANCE. — Calcaire de **12** *St. Ouen*, in Paris basin, lacustrine or brackish (10–20 meters). Calcaire de **13** *Sergy* (Aisne). Grès et mollasse de **14** *Castrais, Mazou, Montespien*, near Narbonne. **15** *Lautrec* (Tarn). **16** *Viviers*, in the Rhone valley. Marnes de **17** *Robiac* (Gard). Sidérolithique de **18** Mormont (in part) near Lyons. Phosphorites de **19** *Quercy* (a small part), in south central France. GERMANY. — Bohnerz von **20** *Heidenheim* (Bavaria). Depéret.

of this age. Of greatest import for our knowledge of the mammals are the marl beds of Robiac (Gard) (17) in south central France, which through the explorations of Depéret[1] have yielded to the Lyons Museum a splendid series of remains of lophiodonts, horses, and other mammals; here was found a veritable bone bed, crowded with well-preserved types.

3. *Ludian Stage.* — This stage is named after the *marnes de Ludes* in the Paris Basin, but is typified by the *gypse de Montmartre* (4), made

[1] Depéret and Carrière, Sur un nouveau gisement de Mammifères de l'Eocène moyen à Robiac près Saint-Mamert (Gard). *C. R. Acad. Sci. Paris*, séa. Oct. 21, 1901, Vol. CXXXIII, no. 17, pp. 616–618.

famous by the classic researches of Cuvier. This stage is equivalent in part to the 'Ligurian' of Mayer; the fauna is readily distinguished from that of the Bartonian by the absence of lophiodonts. The mammals described by Cuvier are from near the summit of the *gypse*. Of the same age are the rich *lignites de la Débruge* (Vaucluse). The best known mammalian life of this period, however, is that of the south of France, as shown in the phosphorites of Quercy (3), the lignites of Gargas (5), and at Euzet (8). In England we have the famous deposits on the Isle of Wight (9), of Hordwell, Bembridge, and Headon. This Ludian fauna is also divided by Depéret [1] into an older phase and a newer phase. We note the presence

FIG. 51. — **Upper Eocene.** Ludian Stage. FRANCE. — **1** *St Hippolyte de Caton* (Gard). Gypse de **2** *Paris* (lower strata). Phosphorites de **3** *Quercy* (in part), south central France. Gypse de **4** *Montmartre*, near Paris, dried up lagoons (55 meters). Lignites, gypse de **5** *Gargas*, southeastern France. Lignites de **6** *Mormoiron* (Vaucluse). **7** *Villeneuve la Comptal*, near Narbonne. **8** *Euzet-les-Bains* (Gard). ENGLAND. — "Barton sand," fluvio-marine, and clays, marls, loams, limestone, sandstone, etc., of **9** *Headon* (140–200 ft.); marls and limestones, "fluvio-marine" of **9** *Bembridge* (120 ft.); "Barton clay" of **9** *Hordwell* (300 ft.), Isle of Wight. Correlation of Depéret.

of the larger archaic carnivores, true members of the family Hyænodontidæ (*Hyænodon, Quercytherium*), also of the type specimen of *Lophiotherium*, a diminutive horse in the same stage of evolution as the American *Epihippus* of the Uinta; that is, with the premolar teeth complicated.

The Upper Ludian, typified by the *gypse de Montmartre* (4) is still more readily distinguished by the first appearance, or at least by our first knowl-

[1] Depéret, C., L'évolution des Mammifères tertiaires (Eocène). 1905.

edge, of several families, including the artiodactyl anoplotheres (*Anoplotherium*) and cænotheres, of the true dogs or Canidæ (*Cynodictis*), and of two previously unknown families of rodents, Theriodomyidæ[1] and Myoxidæ (dormice). More distinctive is the appearance here of diminutive opossums (Didelphyidæ, *Peratherium*), either by migration from North America, or as residents which have not been discovered in older formations.

Mammalian Succession

Cuvier's views restated. — It is interesting to describe the adaptive radiation of the *gypse* fauna so far as possible in the language of Cuvier.[2] The chief animals which he discovered were the palæotheres, which reached their climax at this time, the aberrant artiodactyl anoplotheres, the anthracotheres, Chœropotami, and the lemuroid *Adapis*. The palæotheres were browsers, forest-living animals, resembling tapirs (*P. medium*) in the general form of the body and head, particularly in the shortness of the bones of the nose, which indicate that, like the tapir, they had a short, prehensile proboscis, or upper lip; their grinding teeth are crested like those of the forest-living horses of the Miocene of North America (*Hypohippus*) or of the short-crowned lophoselenodont type. Their resemblance to the forest-living horses is also shown in the presence of three digits on both fore and hind feet. "Our gypsum quarries," observed Cuvier, "are crowded with these animals." The adaptive radiations of the palæotheres are observed first in their size, and second in the variations of the structure of their feet. The largest palæothere (*P. magnum*) was of the size of a horse; another species (*P. medium*) resembles the boar in size and is distinguished by long, narrow feet; a third species (*P. crassum*) is distinguished by its broader feet, and a fourth (*P. latum*) by feet still larger but with shorter digits; a fifth species (*P. curtum*) only attained the size of a sheep, but its feet are still larger and shorter in proportion. The sixth species (*P. minus*), which was attributed to *Palæotherium* by Cuvier, has longer legs and is of a lighter build than the others; it is distinguished by very slender feet, the lateral toes of which are shorter than the median, and is now known under another name (*Plagiolophus minus*). It is famous as having been selected by Huxley as one of the early ancestors of the horse; we now perceive that it was parallel with, rather than ancestral to, the early horses. Cuvier described the anoplothere as of the height of the wild boar, with much-spreading feet and a very long and thick tail, so that as a whole it had nearly the proportions of an otter but with longer legs; it is probable, he said, that it swam well and frequented the lagoons. In widest contrast to these forest and swamp-living forms were the xiphodonts, which, as restored by

[1] Schlosser regards the theriodomyids as primitive hystricomorph or porcupine-like rodents.

[2] Cuvier, G., Discours sur les Révolutions de la Surface du Globe, et sur les Changemens qu'elles ont Produits dans le Règne Animal. Paris and Amsterdam, 1826.

Cuvier, are slender and slightly formed, like the most beautiful gazelles. For the environment of these animals Cuvier pictured a small number of tolerably fertile plains wherein they could multiply, perhaps separated by considerable stretches of lofty hills. The researches of Adolphe Brongniart [1] revealed the flora of the period as consisting of palm trees and many other beautiful plants, while in the waters were found crocodiles and soft-shelled turtles (Trionychia).

The following is a newer picture of the Upper Eocene life of southern France, England, and Bavaria.

Herbivorous mammals. — The odd-toed ungulates, or perissodactyls, become increasingly important. All are polyphyletic, or broken up into a number of independent phyla. (1) The lophiodonts, the dominant family, embrace two main generic phyla (*Lophiodon* and *Chasmotherium*), both descended from Ypresian ancestors, and both becoming extinct in the Bartonian; of these the genus *Lophiodon* splits up into three sub-phyla, according to Depéret. (2) The palæotheres, first known in the Upper Lutetian, also diphyletic and including the cursorial *Plagiolophus* and the less swift but bulkier *Palæotherium*, were of medium size; they become extinct in the Ludian. (3) The hyracotheres, or primitive horses, also subdivided into three and perhaps four phyla (*Pachynolophus, Anchilophus, Lophiotherium*), were of the smallest size and greatest speed. They apparently disappeared from western Europe at the close of the Ludian.

The even-toed ungulates, artiodactyls, though inferior in size to the largest of the perissodactyls, were highly varied and numerous, yet apparently not ancestral to any of the modern artiodactyls. They include: (1) The dichobunes, sub-selenodont artiodactyls of very small size, similar to the homacodonts of North America. This is a prominent Eocene phylum which extends into the Oligocene (Stampian), but according to the best authority (Stehlin) does not give rise to the higher artiodactyls or ruminants.[2] (2) Anthracotheres of somewhat larger size, but swift-moving cursorial forms, first appear in the Lutetian (*Catodontherium*), and destined to survive into the Oligocene (*Brachyodus*), to become dominant in size and variety and to send off branches which migrated to North America. (3) Xiphodonts, excessively light-limbed, fleet, or cursorial forms first known in the Lutetian, surviving to the close of the Eocene (Ludian). (4) Dichodonts and dachrytheres, first appearing in the Upper Lutetian and surviving to the close of the Eocene. (5) Anoplotheres, browsers, forest and swamp dwellers, of larger size, slow-moving, with clumsy feet, first appearing in the summit of the Eocene (Ludian). (6) Aberrant

[1] Cuvier, G., and Brongniart, A., Description Géologique des Environs de Paris. Paris, 1821.

[2] See Stehlin, Die Säugetiere des schweizerischen Eocäns. Critischer Catalog der Materialien. *Abhandl. schweiz. paläont. Ges.*, Vol. XXXIII, Zürich, 1906, Pt. 4, p. 670 (table of the phylogeny of the dichobunids).

suilline, or pig-like, forms (Suidæ) embracing the larger form *Chœromorus*, and *Acotherulum*, of diminutive size.

Chief Mammals
Lophiodonts
Palæotheres
Hyracotheres
(primitive horses)
Dichobunids
Anthracotheres
Ancodonts or hyopotamids
Xiphodonts
Dichodonts
Anoplotheres
Suillines
Lemuroids
Sciuroids
Moles and hedgehogs
Hyænodonts

The most striking fact regarding this assemblage of mammals is that so few of them are ancestral to the Oligocene mammals of the same geographic, region. This is seen in the special study of several of the groups.

Three phyla of Eocene suillines. — We are indebted to Stehlin for a masterly review[1] of the descent of the Eocene suillines of Europe. The key to the interpretation of these mammals, which have been in confusion since the time of Cuvier, is found in the discrimination of three grand phyla and several subphyla, readily distinguished by four characters, namely, through their respective dolichocephaly or brachycephaly, the shape of the posterior part of the mandible, the arrangement of the anterior, or cutting teeth, and the presence or absence of a mesostyle on the superior grinders. Thus *Chœropotamus* (dolichocephalic), *Chœromorus* (mesaticephalic), *Cebochœrus* (brachycephalic) represent three distinct lines, widely spread geographically and of great geologic range, from the Upper Lutetian to Lower Sannoisian. No suoids are known from the Lower Lutetian, and *Chœropotamus* alone survives into the Lower Sannois an. Only *Leptacotherulum* of Quercy and *Chœromorus* of Mormont remain as a possible source of Oligocene evolution. Through the aberrant evolution of their cutting teeth neither *Chœropotamus* nor *Cebochœrus* can include ancestors of the post-Eocene suillines. Stehlin suggests that they may be ancestral to the hippopotami, which first appear in the Lower Pliocene of Europe.

Five phyla of Eocene anthracotheres. — These animals, large and small, are readily distinguished from the pigs by their selenodonty, *i.e.* all the outer and often the inner crests of the superior grinding teeth are crescentic. In this connection it is interesting to note that the pigs also originally possessed crescentic cusps, that their rounded cusps are secondary, or neobunodont.[2] Among the smaller anthracotheres (*Haplobunodon*, *Rhagatherium*) of Egerkingen, Mormont, Hordwell, Bembridge, and Quercy (of Lutetian to Ludian age), as well as *Lophiobunodon* of Lissieu and La Levinière, we discover five phyla which suddenly make their appearance in Upper

[1] Stehlin, H. G., Die Säugetiere des schweizerischen Eocäens. Critischer Catalog der Materialien. Fünfter Teil: Chœropotamus, Cebochœrus, Chœromorus, Haplobunodon, Rhagatherium, Mixtotherium. *Abhandl. schweiz. paläont. Ges.*, Vol. XXXV, 1908, pp. 691–837.

[2] Stehlin, H. G., Über die Geschichte des Suiden-Gebisses. *Abh. schweiz. paläont. Ges.*, Vols. XXVI–XXVII, 1899, 1900, Pt. 1, p. 125.

Lutetian times, because no anthracotheres are known below this period, and no similar forms are found in the Eocene of North America. None of these European forms appear to include the ancestors of the true Oligocene anthracotheres (*Anthracotherium*) of Europe, a case of discontinuity which is parallel to that of the Eocene and Oligocene pigs. Stehlin concludes that the anthracotheres occurring in the Lower Oligocene of Europe are not autochthonous, but migrants, or "in-wanderers." Since almost simultaneously similar "in-wanderers" appear in North America, we should probably regard Asia as the common northern center of the true anthracotheres; still, we must not forget that the diminutive (*Rhagatherium ægyptiacum*) form of the Fayûm of northern Africa is one of the most primitive anthracothere types which we know.

Ancodonts. — Parallel with and related to the anthracotheres is the second group of semi-selendont artiodactyls which, in a comprehensive sense, can be embraced in the term Eocene *ancodonts*, or hyopotamids, distinguished by the structure of the molar teeth, the open mesostyles, and the generally sharpened crests. These Eocene ancodonts are astonishingly numerous, including *Mixtotherium* (brachycephalic) from Quercy, and *Dacrytherium* (dolichocephalic), and ranging through the Lutetian, Bartonian, and Ludian stages in several phyla, including beside, the above *Catodontherium* and *Hyracodontherium*. While these animals (*Mixtotherium*) disappear at the close of the Eocene of Europe, Stehlin discusses the very interesting question, already suggested by Scott (1890) and Earle, of their possible ancestry to the group of oreodonts which suddenly appear (*Eomeryx, Protoreodon, Protagriochœrus*, etc.) in the Uinta Formation, Upper Eocene, of northern Utah, Rocky Mountains. Stehlin, however, dismisses this theory, showing that, despite many resemblances, the mixtotheres of Europe are too specialized to have given rise to the oreodonts. He admits the possibility of a north Asiatic center from which common ancestors of the European mixtotheres and the American oreodonts may have wandered, to give rise to the respective Old and New World forms.

Arboreal mammals. — The Primates include the lemur-like *Adapis*, appearing in the Lutetian, surviving through the Ludian, and reappearing in the giant *Megaladapis* of Madagascar. There is also the *Tarsius*-like *Necrolemur*, which appears in the Lutetian and survives through the Ludian.

Of arboreal type are also probably the sciuromorph, or squirrel-like rodents (*Plesiarctomys*), analogous to similar forms in North America; it is noteworthy that most Eocene rodents seem to be arboreal or forest-living forms; the plains-living forms are not known until the Oligocene. Of the remaining small fauna it is important to note that among Insectivora both the moles (Talpidæ) and hedgehogs (Erinaceidæ) first appear in the Lutetian.

Considering this powerful herbivorous and small fauna it is surprising that we know so little of the carnivores, since these are confined to the small viverroid, or *Sinopa*-like forms of the Lutetian, which are succeeded by the

true *Hyænodon* of the Bartonian and Ludian. Northern Asia or Eocene Europe appears to have been the home of the genus *Hyænodon*, because these animals do not appear in northern Africa and in North America

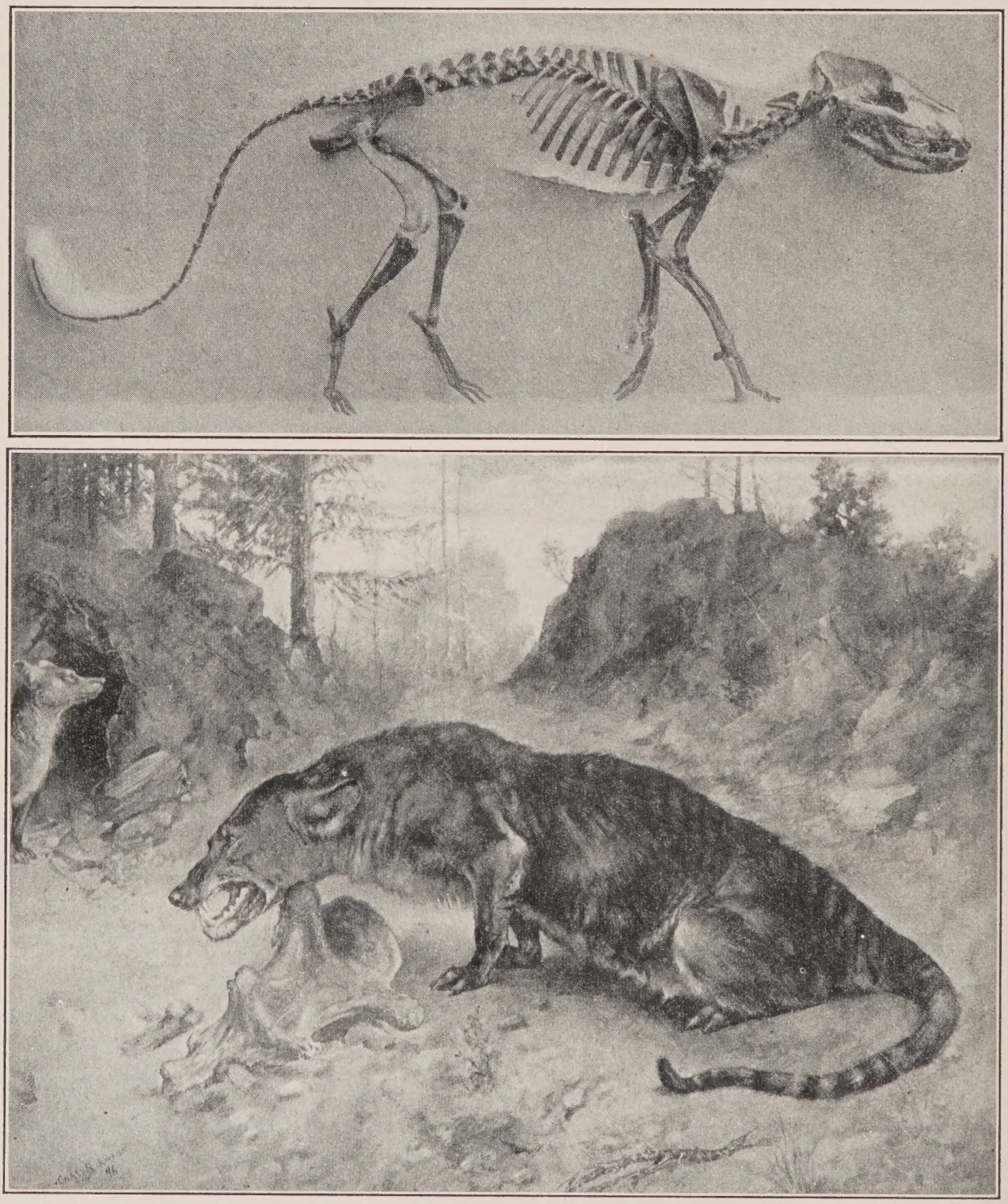


FIG. 52. — The New and Old World family of mesonychid creodonts, known in the Lower Eocene of Europe and in the Lower to Upper Eocene of North America. Above : Skeleton of the Middle Eocene (Bridger) *Dromocyon vorax*, in the Yale Museum. Below : Restoration of a similar form. After original by Charles R. Knight, in the American Museum of Natural History.

until the Lower Oligocene. They are typically cursorial or running creodonts or primitive carnivores, capable of traveling great distances, and thus finally enjoying a very wide geographic range, before extinction.

The Collective Fauna of the Phosphorites of Quercy

The beginning of these fissure deposits occurred during Bartonian times; they richly display the life of the Upper Eocene or Ludian stage, and extend into the totally different mammalian fauna of Middle Oligocene or Stampian times, thus representing a very long period of time. They are the most extensive and famous mammal-bearing fissure deposits which have ever been discovered. They are found in Jurassic calcareous fissures, 3 to 6 meters in width and 35 meters in length; the matrix is a phosphate of lime, probably of mineral spring origin. The mammalian fauna is of extraordinary richness, beauty, and completeness. Gaillard [1] considers that the *phosphorites* were formed as a result of alternation of wet and dry seasons, such as we see in the tropics to-day; tricklings of rain water filled crevasses in the rocks and became saturated with the dissolving limestone; this process was followed by the advent of the dry season, a period of evaporation, during which the *phosphorites* were precipitated. The mammals often occur entire, as in caverns to-day. Filhol,[2] in his monograph, suggested that death was caused by asphyxiation due to poisonous vapors rising from the hot springs.

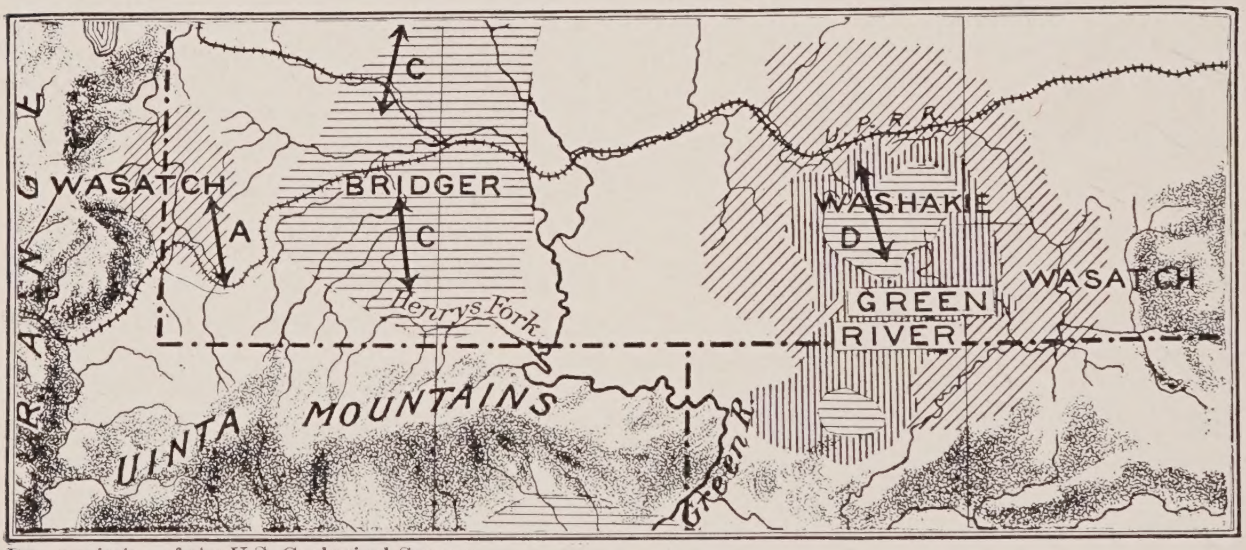
The birds of Quercy. — The recent studies by Gaillard [1] on the bird life preserved in these fissures throws a very important side light both on the climatic condition of the period and the zoögeographic relations of France at this time, that is, between the Middle Eocene and Middle Oligocene. The birds, like the mammals, of the *phosphorites* show so little resemblance to those of the present day that very few can be referred to living genera. They are all types fitted to inhabit great warm plains, scattered with groves. They can be referred to the following groups: diurnal and nocturnal birds of prey (Raptores); the American vultures (Cathartidæ); the serpenteaters (Serpentariidæ), of which the existing African 'secretary bird' is the only existing form; the storks (Ciconiidæ); the sandpipers (Totaninæ); the rails (Rallidæ); the Old-World quails (Perdicinæ); the Asiatic and African sand grouse (Pteroclidæ); and the rollers (Coraciidæ), cuckoos (Cuculidæ), goat-suckers (Caprimulgidæ), and swifts (Cypselidæ) of the large group Pico-passeriformes. Entirely lacking are several families of aquatic birds and probably the true sparrows. It is an essentially tropical assemblage. The descendants of the Quercy birds, or at least such forms as approach them most closely, are now for the most part inhabitants of the equatorial regions of Africa and South America. Thus the serpenteaters, the gangas, or sand grouse, the gallinaceous birds of the genus *Palæocryptonyx*, the rollers (*Geranopterus*), and the touracos (*Dynamopterus*) lend to the Quercy fauna an African or Indo-Malayan aspect. On the other hand, there are forms

[1] Gaillard, C., Les Oiseaux des Phosphorites du Quercy. *Ann. Univ. Lyon*, n.s., I, Sci. Med., no. 23, 1908.

[2] Filhol, H., Recherches sur les Phosphorites du Quercy, Paris 1877, p. 127.

with distinctly American affinities. *Plesiocathartes* is related to the tropical American king vulture (*Sarcorhamphus*); *Orthocnemus* approaches the Brazilian chaha (*Chauna chavaria*); *Elaphrocnemus* approaches the 'quadruped bird,' or hoatzin, of Central America, and *Filholornis*, the penelopes (Penelopinæ), likewise of Central and South America. The striking relationship that exists between certain birds of the *phosphorites* and living American forms justifies the assumption that there were intermigrations of New World types during the Eocene or Oligocene.

Eocene birds of North America and Europe. — It is interesting at this point to refer to the little that is known of Eocene birds of North America.[1] Of the Lower Eocene the *Diatryma gigantea* of the Wasatch of New Mexico



By permission of the U.S. Geological Survey.

FIG. 53. — Chief Middle Eocene Formations (horizontal lines). Bridger, C C, of southwestern Wyoming. Washakie, D, of south central Wyoming.

is a large flightless bird, possibly related to the genus of the same name in England and France. The various species of *Aletornis* described by Marsh are believed to be allied to the cranes. They vary from the size of the killdeer plover to that of a flamingo. The owls (*Bubo*) and woodpeckers (*Uintornis*) are also provisionally identified. The few records we possess of the birds of undoubted Eocene age in England and France point in the same manner to early differentiation of bird life. In the Lower Eocene, or Sparnacian of northern France, Belgium, and England, the giant *Gastornis* is abundant, an animal as large as an ostrich, not a true struthious type, however, but presenting rather affinities to the wading and aquatic birds. In the Lower Eocene, or Ypresian, of the Isle of Sheppey, small vultures (*Lithornis*), kingfishers (*Halcyornis*), sea gulls, and herons have been found.

From the Upper Eocene of Montmartre Cuvier recognized eleven distinct species. Altogether there were representatives of the Accipitres, or birds of prey, of the Passeres, or tree perchers, of the Picariæ, including the wood-

[1] American Ornithologists' Union (J. A. Allen, Editor), Check-List of North American Birds, 3d and revised ed. New York, 1910.

peckers, cuckoos, rollers, etc., the Gallinæ, or gallinaceous birds, the Grallæ, or shore-frequenting birds, and finally of the Steganopodes, which include the cormorants.[1]

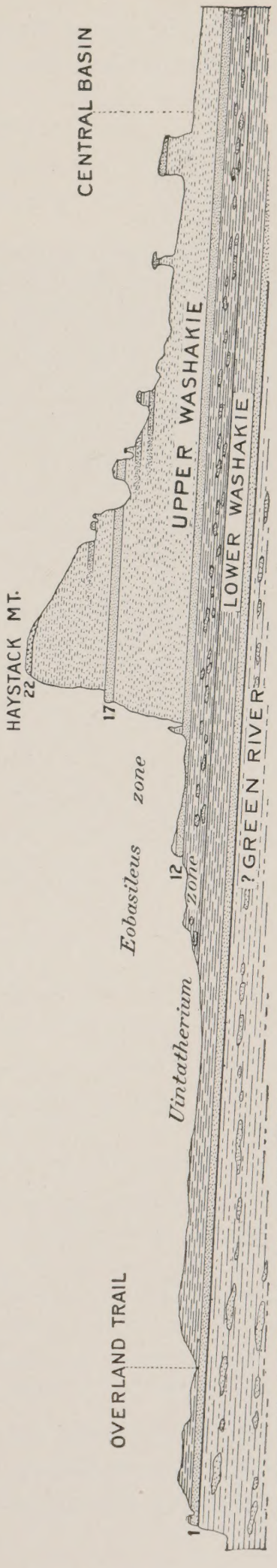
Middle and Upper Eocene of the Rocky Mountain Region

The whole vertebrate fauna, reptilian as well as mammalian, of this period is better known than that of any other of the Eocene phases. As shown in the correlation table (Fig. 10, p. 49) the Middle and Upper Eocene is represented by a grandly successive series of formations, partly overlapping in time, and apparently leaving no interval unfilled with records of mammalian life. Reading from the base upward, these formations succeed and overlap each other as follows:

Uinta, of northern Utah, including three levels
Washakie, of south central Wyoming, including two levels
Bridger, of southwestern Wyoming, including two main levels
Huerfano, of southeastern Colorado, including two levels.

Mammalian life. — Like the Middle and Upper Eocene of Europe, the mammalian life of the Rocky Mountain region of North America is a unit. Of the twenty-six families of mammals of every kind, seven cease to be known at the end of the Middle Eocene or Upper Bridger phase. Only two new families are suddenly introduced at the summit of the Eocene or Upper Uinta phase. There was thus in the Rocky Mountain region a long period of uniform evolution and competition among the members of the existing fauna, a few families becoming extinct and the majority surviving with no sudden introductions of dangerous competitors. On

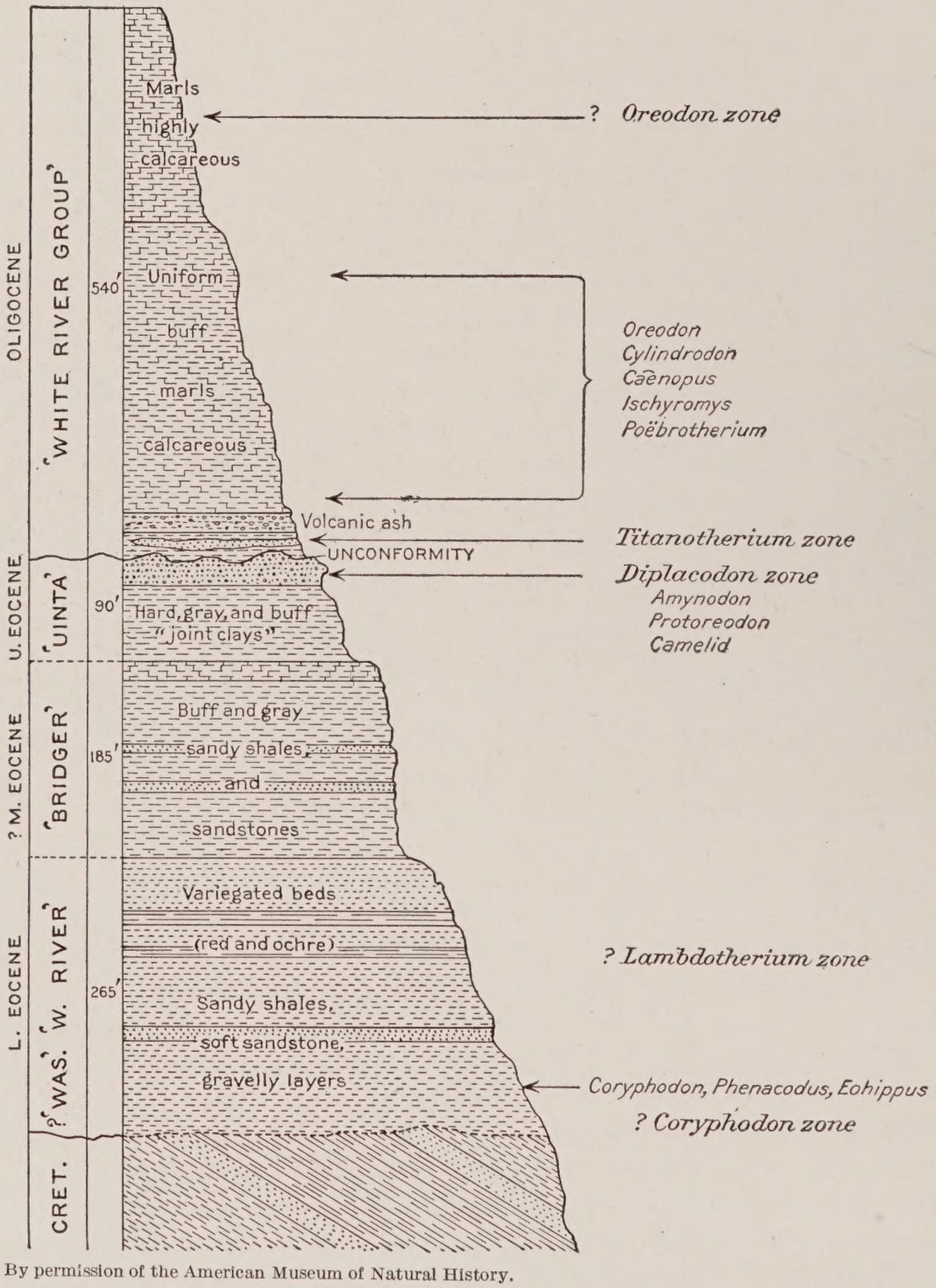
[1] Owen, Palæontology (1860), pp. 291–292.



By permission of the American Museum of Natural History.

Fig. 54. — Middle and Upper Eocene section (not in scale series) of the Washakie Formation overlying the Green River (= Lower Bridger, in part) in central Wyoming. After Granger, 1909.

the whole, it is a very imposing, diversified, and well-balanced fauna, with an equal distribution of arboreal, cursorial, aquatic, fossorial, carnivorous, and herbivorous types.



By permission of the American Museum of Natural History.

FIG. 55. — Lower Eocene to Oligocene. A composite, continuous section in the Wind River Basin, Wyoming. After Granger, 1910. Compare Fig. 38.

As above noted, the chief distinction from Europe is in the large proportion of surviving archaic Mammalia. Very noteworthy is the presence of an opossum (*Peratherium*) as indicating the continued residence of

polyprotodont marsupials in this country. Among the Carnivora-Creodonta, we find three families, the oxyænids, hyænodontids, and mesonychids, the last developing into animals of formidable size.

The Insectivora are highly varied, including six families, four of which are now extinct, while two are doubtfully compared with the modern moles (Talpidæ) and tenrecs (Centetidæ) as well as with the tupaiids or

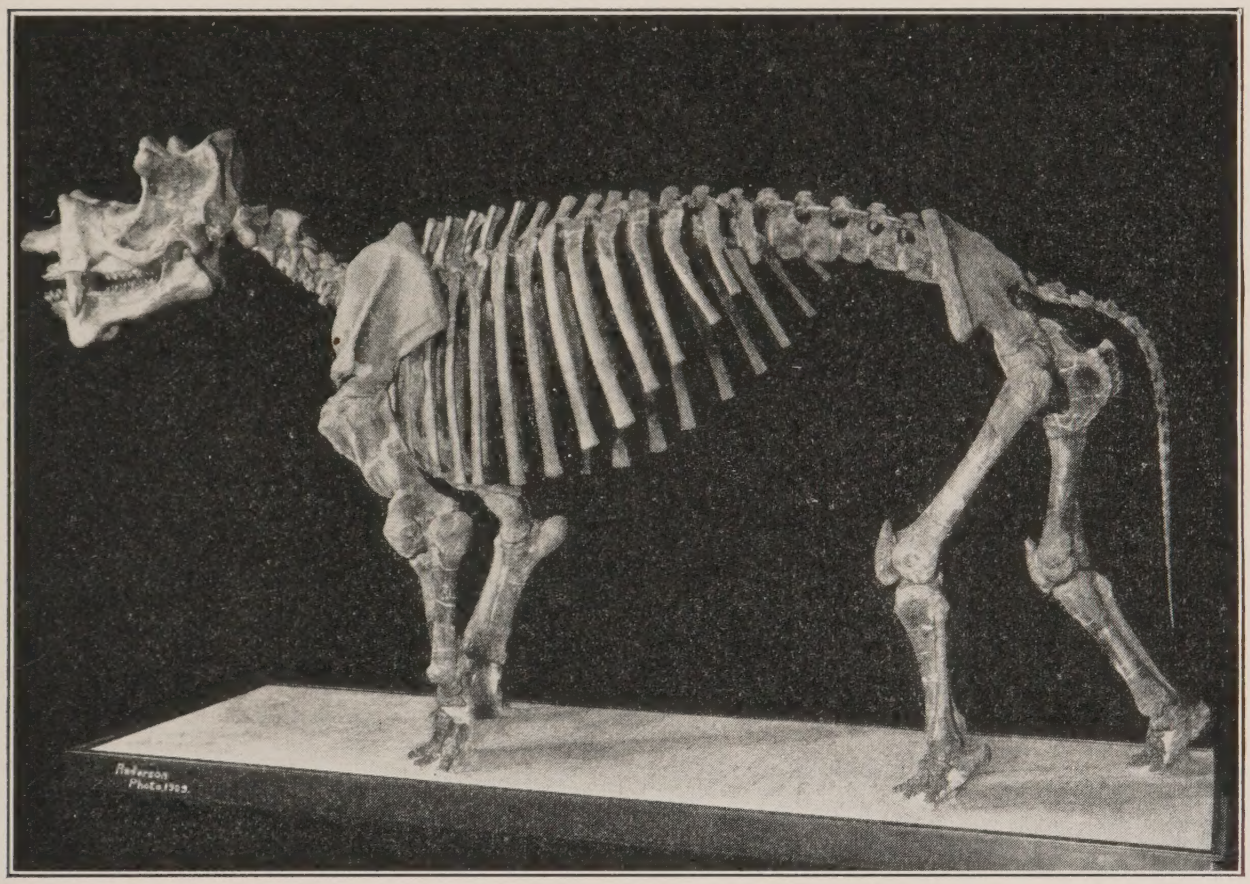


FIG. 56. — Skeleton of *Uintatherium* (*mirabile*), the amblypod successor of *Pantolambda and Coryphodon*. Uintatherium Zone, Upper Bridger. (See Fig. 58.) In the American Museum of Natural History. After Osborn.

tree shrews. The peculiar herbivorous Tillodontia apparently become extinct in *Tillotherium* of the Bridger. The archaic edentates with enameled teeth (Tæniodonta) survive into the Lower Bridger only (*Stylinodon*). Of the archaic Ungulata the phenacodonts have all disappeared, but the amblypod stock is apparently flourishing and reappears in the imposing *Uintatherium* of the Middle Bridger. In the Middle Eocene the ratio of archaic and modernized genera and species of mammals is as follows:

	Genera	*Species*
Archaic mammals	15	35
Modernized mammals	57	146
	72	181

Thus there is for the first time a decided predominance of the modernized over the archaic forms. Among what we have been regarding as the more modern types, the arboreal primates now include two families (Anap-

tomorphidæ, Notharctidæ), both surviving from the Lower Eocene. The pro-Carnivora (Miacidæ) also survive from the Lower Eocene, and become more diversified than in the Wind River, although most of the genera are modified Lower Eocene forms. The Rodentia still are limited to the rather generalized Ischyromyidæ, also surviving from the Lower Eocene and becoming diversified into six genera, which may prove to represent more than one family. At the very summit of the Eocene the American rodents known as jumping mice, or Dipodidæ, are doubtfully represented in the genus *Protoptychus*. Among the modern ungulates, as in Europe, this is the grand epoch of the Perissodactyla. Of these, two families only (Equidæ and Lophiodontidæ) have relatives in Europe. Of the remaining families, the tapirs (Tapiridæ), titanotheres (Titanotheriidæ), two families of rhinoceroses (Hyracodontidæ, Amynodontidæ), cursorial, aquatic, or amphibious respectively, appear to be peculiar to North America.

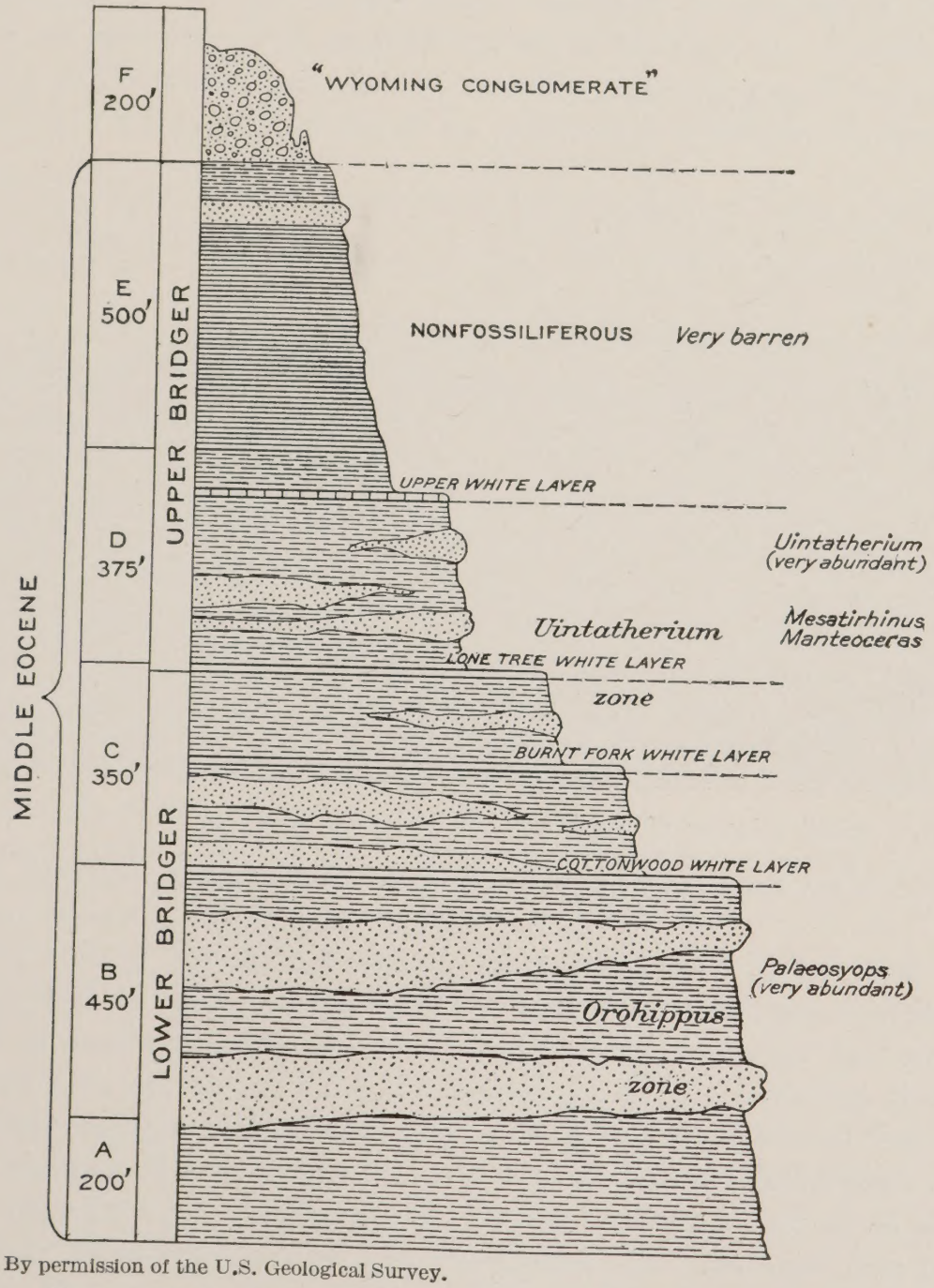
CHARACTERISTIC MAMMALS

Uintatheres
Horses
Tapirs
Rhinoceroses
Titanotheres
Lophiodonts
Entelodonts
Homacodonts
Oreodonts
Camelids
Tæniodonts
Tillodonts
Insectivores
Lemuroids
Armadillos

The even-toed ungulates, or Artiodactyla, are far less diversified than in Europe. They include the bunodont and omnivorous Achænodontinæ (*Achænodon*), related to the entelodonts

FIG. 57. — In the heart of the Middle Eocene, Bridger Badlands of Wyoming, in the famous locality known as Grizzly Buttes. Zone of *Orohippus* and *Palæosyops*. Photograph by American Museum of Natural History, 1903.

(see p. 217) or 'giant pigs,' which are destined to play a very imposing part in the Oligocene of North America and Europe. The diminutive selenodonts (*Homacodon*), provisionally referred to the European family of Dichobunidæ, may represent an independent family (Homacodontidæ). The most novel American forms, also destined to be conspicuous in the



By permission of the U.S. Geological Survey.

FIG. 58. — Typical Middle Eocene of western Wyoming. Scale section of the Lower and Upper Bridger Formation. Prepared by Matthew and Granger, 1903.

future history of the continent, are the oreodonts (Oreodontidæ) and the pro-camels (Camelidæ or Hypertragulidæ).

Geology of the Middle Eocene Bridger, Lower Washakie, and Lower Uinta Bridger. — These noble exposures in southwest Wyoming, discovered in 1869, are the classic hunting grounds of Leidy, Marsh, and Cope, famous

for a rich fauna, and of late most accurately surveyed by the American Museum parties.

Clarence King [1] believed that the Bridger and Washakie deposits (Fig. 35, p. 118) were formed in a great single or partly divided 'Washakie Lake.' This long accepted lacustrine theory has gradually given way before the arguments of Matthew [2] and Davis [3] for the flood plain and fluviatile theory. It is definitely shown (Osborn, Granger) that the Washakie Formation began during the Upper Bridger, but continued on after the Bridger ceased. In both formations, as shown by the studies of Sinclair [4]

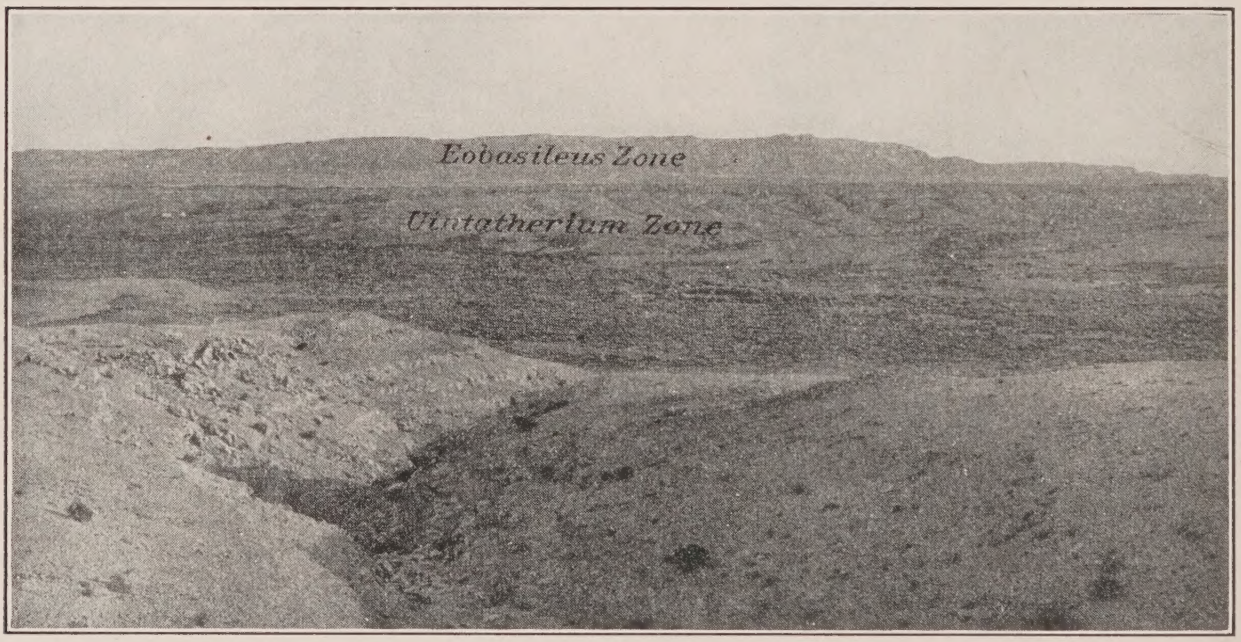


Fig. 59. — Middle Eocene of the Washakie Basin, Wyo., Haystack Mountain or 'Mammoth Buttes.' Lower: top of Middle Eocene or Uintatherium Zone. Upper: base of Upper Eocene or Eobasileus Zone. Photograph by American Museum of Natural History, 1906.

and the analyses of Johannsen, volcanic ash, ejecta, and erosion materials are important ingredients, so that we may imagine that in Bridger times this basin was surrounded by active volcanoes, as represented in Fig. 23, which lent grandeur to the landscape. From his observations while collecting fossil turtles in the Bridger in 1903, Hay [5] concluded that the Bridger deposits were almost solely the result of fluviatile and flood plain action, that this basin was a nearly level country, probably covered with vegetation and well forested. The occurrence of fossil remains in all portions of the Bridger beds indicates that there existed no permanent sheet of

[1] Clarence King, Systematic Geology, Washington, 1878, p. 458.

[2] Matthew, W. D., Is the White River Tertiary an Eolian Formation? *Amer. Natural.*, Vol. XXXIII, 1899, pp. 403–408.

[3] Davis, W. M., The Fresh-water Tertiary Formations of the Rocky Mountain Region. *Amer. Acad. Arts and Sci., Proc.*, Vol. XXXV, 1900, pp. 346–373.

[4] Sinclair, W. J., Volcanic Ash in the Bridger Beds of Wyoming. *Bull. Amer. Mus. Nat. Hist.*, no. 22, 1906, pp. 273–280.

[5] Hay, O. P., The Fossil Turtles of the Bridger Basin. *Amer. Geol.*, Vol. XXXV, June, 1905, pp. 327–329.

water. There can be little doubt that most of the animals lived near the places where they were buried. They are such forms as would be found in a well-wooded region. In the channel beds, composed of

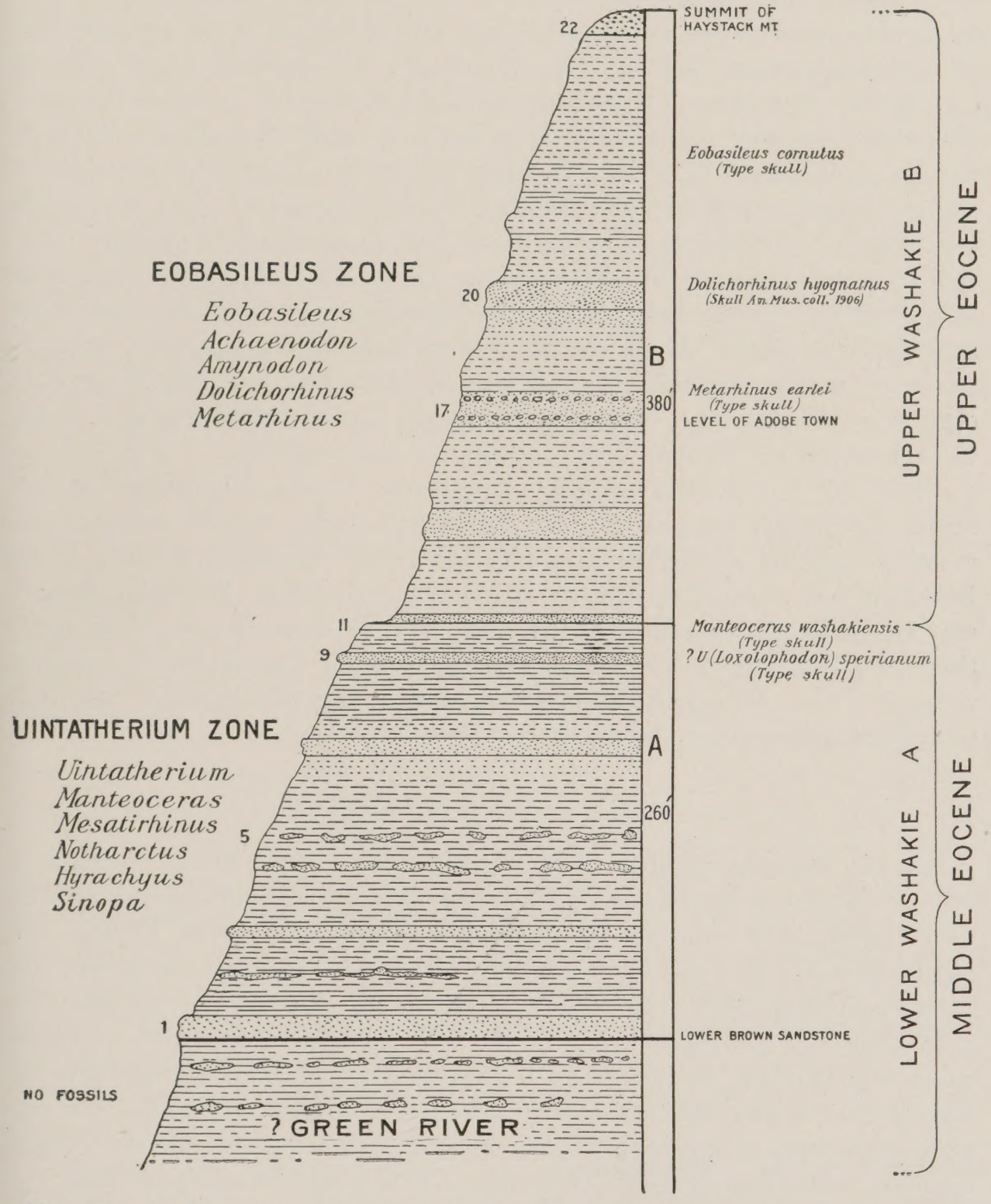


FIG. 60. — Section (not in scale series) of Lower and Upper Washakie of central Wyoming, showing distribution of the principal types of mammals. Prepared by Granger, 1907.

coarse materials, there is proof of streams with rapid currents traversing the basin, bordered by swamps in which were formed beds of lignite, or by freshwater bays in which the Unionidæ, or freshwater mussels, accumulated. While the coarse deposits indicate streams, finer deposits indi-

cate mud beds, or shallow water conditions, in which the remains of uintatheres and rhinoceroses are occasionally found as if they had been mired in a standing position (*Hyrachyus* has been found in this way). Occasionally, however, the entire region must have been flooded for long periods, because the careful researches of Granger and Matthew reveal the existence of successive 'white layers' (Fig. 58) of great horizontal extent, largely calcareous, or composed of shallow limestone containing shells (*Goniobasis, Planorbis*), as well as weatherworn jaws of small mammals. In their harder constituency these layers form the caps of the great benches or steppes which subdivide the grand Bridger Formation into successive layers, A — F. These hard layers also serve to mark off the Bridger into faunal levels. In general on the lower levels we find smaller mammals in lower stages of evolution, while on the higher levels we find larger mammals in a more advanced stage. There is thus a general progression and advance of mammalian life from below upward, and secondly a gradual change in the character of the fauna, partly due to extinction and partly to invasion of the Bridger from the surrounding country.

Washakie. — The Washakie lies fifty miles east of the Bridger, a formation occupying an area of over 300 square miles, chiefly composed of volcanic material and subdivided into the Lower Washakie (Brown Beds, Uintatherium Zone, 260 feet in thickness) and Upper Washakie (Green and Gray Beds, Eobasileus Zone, 380 feet in thickness). First mentioned by Hayden in 1869,[1] it is famous through the successive explorations of Cope, Marsh, Scott, Osborn, and finally of Granger,[2] who has solved its geologic and faunal characters.

Fish and Reptile Fauna

In the stream channels of the Bridger have been found remains of several species of bowfins (Amiidæ) and garpikes (Lepidosteidæ) as well as of catfishes or siluroids (*Rhineastes*). From the Lower Bridger are also described three species of snakes. The crocodiles were numerous and diversified, including *Crocodilus* as well as the diminutive *Limnosaurus* with laterally compressed teeth. Several species of Lacertilia (*Glyptosaurus*) have been described. All these partially known reptiles give us hints as to the Floridian or south temperate conditions of climate, and the great abundance of aquatic life. We may picture partly open, partly forested country, somewhat similar to the bayou region of the Mississippi Delta.

More direct information is afforded from Dr. Hay's monographic studies on the Testudinata.[3] We might expect to find here representa-

[1] Hayden, *op. cit.*, 1869.

[2] Granger, W., Faunal Horizons of the Washakie Formation of Southern Wyoming. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVI, no. 3, Jan. 19, 1909, pp. 13–23.

[3] Hay, O. P., The Fossil Turtles of North America. *Publ. Carnegie Inst.*, Washington, no. 75, 4to, 1908.

tives of the characteristically South American order of side-necked or pleurodiran turtles, but such have not been found. The soft-shelled river turtles (Trionychoidea) were represented by at least two species, whereas there are at present in the whole world only twenty-six; the Bridger rivers and brooks fairly swarmed with these creatures, some of them equal in size to the largest existing Asiatic species. They are indicative of flowing waters. Swampy conditions are indicated by the presence of fourteen species of the family Emydidæ (order Cryptodira), as compared with the twelve species living in the Mississippi valley to-day. The genus *Baptemys* of the same order has its nearest relatives at present in Central America, while a third genus (*Anosteira*) is reported by Lydekker in the Upper Eocene of England. The presence of extensive stretches of land is indicated by the true land tortoises (Testudinidæ) of the genus *Hadrianus*, including giant tortoises nearly three feet in length, which probably lived on dry lands bordering the Bridger Basin. The ancient, Lower Cretaceous order Amphichelydia is also represented here by four species belonging to two genera.

The Succession of Middle Eocene Mammals

Lower Bridger or Orohippus Zone. — The Lower Bridger includes levels A, B, C, of the section Fig. 58. It is characterized by the *absence* of the Amblypoda. It may be distinguished as the *Orohippus Zone* from the presence of these characteristic little 'mountain horses.'

Many older Wasatch and Wind River species are found on this level which do not survive into the Upper Bridger. All the creodonts and pro-Carnivora are of older type. The Insectivora, Primates, and smaller Carnivora are richly represented in the locality known as Grizzly Buttes. Here have been found among the monkeys, or lemurs, the *Tarsius*-like anaptomorphids, the notharctids, resembling some of the South American monkeys, as well as remains of *Microsyops* with its rodent-like incisors, analogous to those of the aye-aye of Madagascar. There is also the long-tailed and probably aquatic insectivore *Pantolestes*, and numerous minute, shrew-like insectivores. Opossums (*Peratherium*) also occur. The primitive hyænodonts *Sinopa* and *Tritemnodon* abound in these lower beds. *Mesonyx* is a Lower Bridger animal.

Among the hoofed mammals or ungulates the delicate lophiodont *Helaletes* is most common, analogous to the *Chasmotherium* of France. Among the horses five species of *Orohippus* occur, all animals of small size and still possessing four digits on the fore feet. Among titanotheres principally the broad-headed *Palæosyops* and *Limnohyops* occur in relatively early stages of evolution. It is noteworthy that no traces of horns are found upon the heads of the titanotheres on this level. The prorhinoceroses, or hyracodonts, are represented only by the light-limbed

Hyrachyus. The tapirs have not as yet been discovered in the Lower Bridger. The mammal of most exceptional interest is the armadillo

FIG. 61. — Outline restorations to same scale ($\times \frac{1}{20}$) of contemporary Middle Eocene mammals. By Charles R. Knight. *A. Notharctus*, a primate, arboreal. *B. Orohippus*, a primitive horse, cursorial. *C. Hyrachyus*, a primitive rhinoceros. *D. Tillotherium*, a tillodont. *E. Dromocyon*, a creodont, cursorial. *F. Palæosyops*, a titanothere. *G. Metacheiromys*, an armadillo, ambulatory. *H. Patriofelis*, a creodont.

Metacheiromys, similar in many respects to the smaller existing armadillos, but apparently possessing a leathery instead of a bony shield, the jaws lacking the columnar enamelless teeth of the existing *Dasypus*, but defended

in front by a pair of sharp caniniform teeth coated with enamel. The archaic edentate *Stylinodon* is doubtfully represented in this level. The tillodont stage is *Trogosus*.

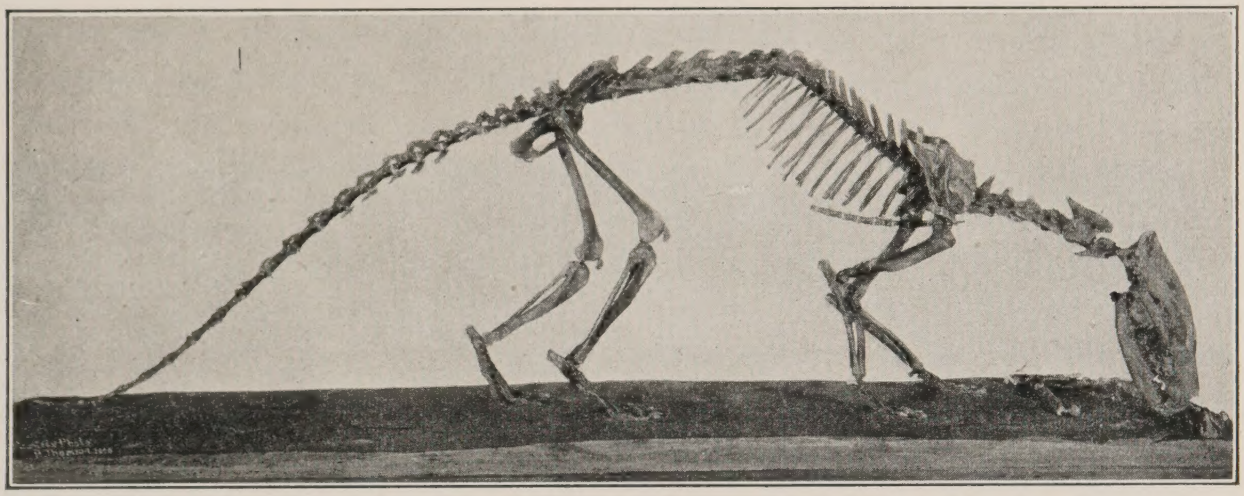


FIG. 62. — A destroyer of Middle Eocene smaller mammals and birds. Skeleton of the slender-limbed creodont *Tritemnodon agilis*. In the American Museum of Natural History.

Upper Bridger Levels C and D, Lower Washakie and Lower Uinta. — The geographic distribution of these contemporaneous depositions is displayed on the map on p. 120.

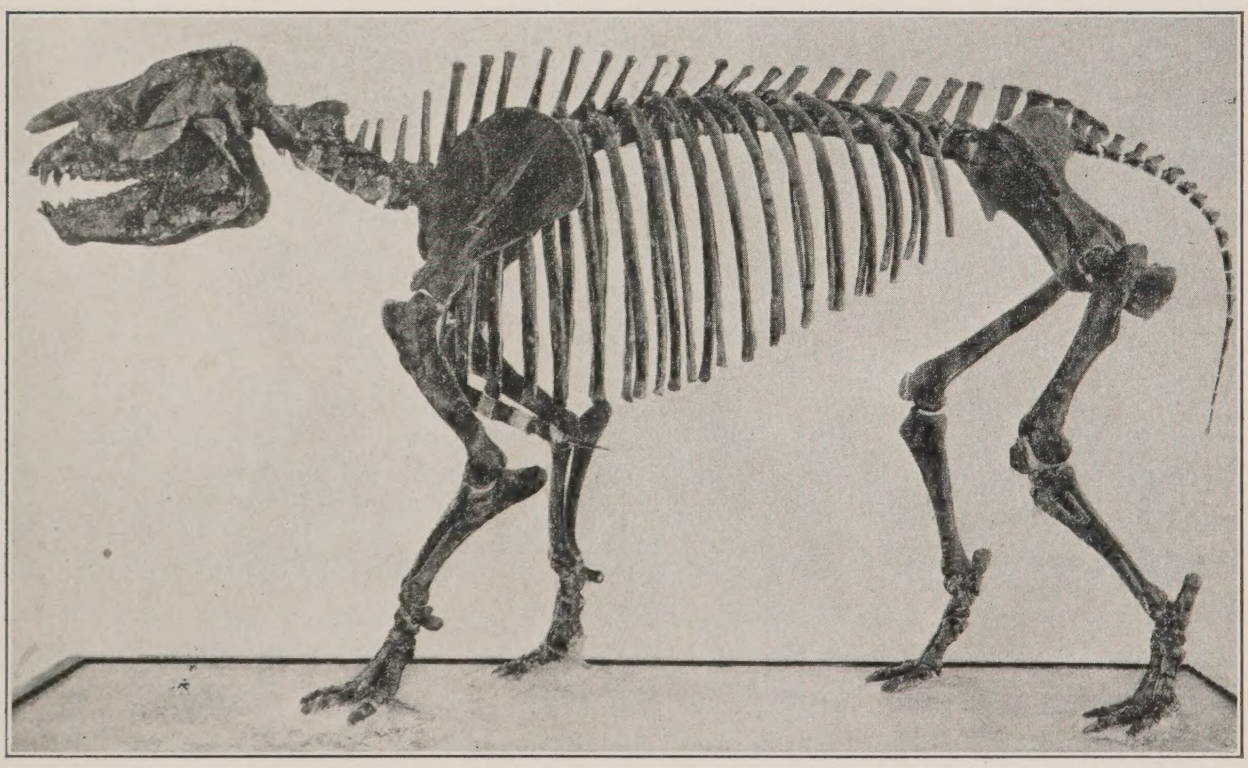


FIG. 63. — Skeleton of the Middle Eocene tapir-like titanothere *Palæosyops leidyi*. One of the large mammals of the Orohippus zone. In the American Museum of Natural History.

(1) *Upper Bridger: Uintatherium Zone.* — This level is marked by the introduction of a number of new forms, including especially the great amblypod Dinocerata, which are represented by species of *Uintatherium* in various stages of evolution. These animals differ from *Coryphodon* in

the absence of upper cropping teeth, and in the presence of spear-like tusks and two pairs of prominent osseous horns. The body is intermediate in proportion between those of the elephant and rhinoceros. The feet are extremely short and broad. The brain (Fig. 71) is no larger than that of a dog, out of all proportion to the body, and essentially of the archaic type. These animals are very abundant both in the Upper Bridger and Lower Washakie, and serve to tie these formations into a single life-zone.

Of the creodont Carnivora the small hyænodont *Sinopa* is becoming somewhat more rare. The large, powerful creodont *Patriofelis* of the family Oxyænidæ, analogous in its proportions on a powerful scale to the modern wolverine (*Gulo*), and in its dentition to *Hyæna* and *Synoplotherium*, was capable of attacking the largest contemporary mammals. Here also the skulking and swift-footed *Mesonyx* (or *Dromocyon*, Mesonychidæ) is represented by species of intermediate size (Fig. 52). Of the modernized

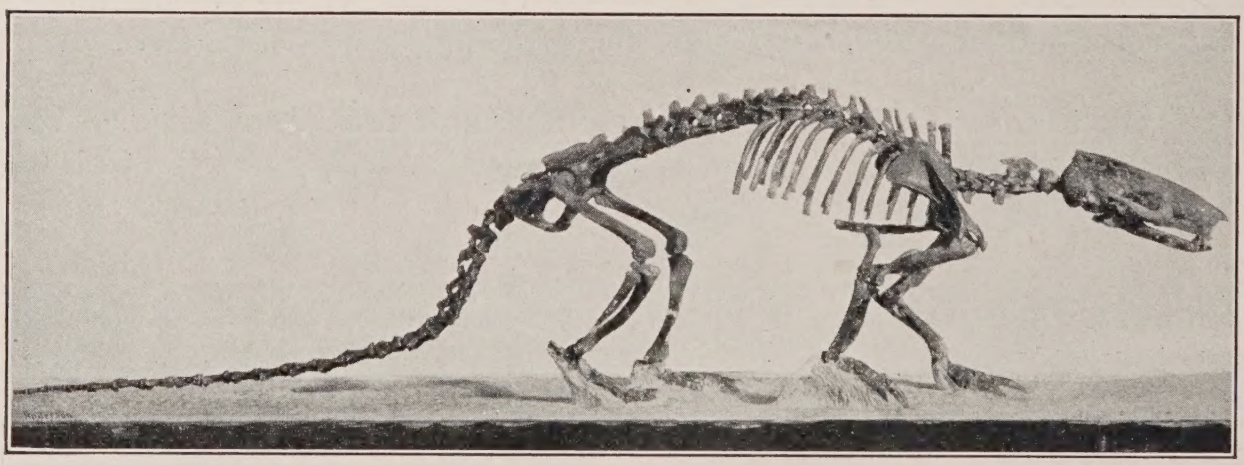


Fig. 64. — The armadillo in North America. Skeleton of the Middle Eocene *Metacheiromys tatusia* of the Bridger formation. In the American Museum of Natural History.

ungulates the tapirs (*Isectolophus*) occur, but are rare. The horses (*Orohippus*) as well as the primates (Notharctidæ) are in a somewhat more advanced stage of dental evolution than in the Lower Bridger levels. The titanotheres now become polyphyletic through the appearance of three additional phyla (*Telmatherium*, *Manteoceras* and *Mesatirhinus*) in addition to the extremely broad-headed *Palæosyops* Thus indications of at least five phyla of titanotheres now occur, including long-headed forms with more hypsodont teeth, and short-headed forms with more brachyodont teeth. Of great interest is the development of rudimentary horns on the forehead above the orbits, which appear as 'rectigradations,' in all of these phyla.

(2) *Lower Washakie: Uintatherium Zone.* — The Lower Brown Beds of the Washakie contain a fauna identical with that of the Upper Bridger C and D, namely, *Uintatherium*, *Palæosyops*, *Manteoceras*, *Mesatirhinus*, *Notharctus*, *Hyrachyus*, and *Sinopa*, in fact, the genera of the Lower Washakie are almost without exception found in the Bridger and are represented

by species closely allied to those of the Upper Bridger and in some cases identical with them. None of these genera, however, excepting the insectivore *Hyopsodus* and the rodent *Paramys* survive into the Upper Uinta. A similar fauna is contained in the little-known Lower Uinta beds, south of the Uinta Mountains. These three levels (Upper Bridger, Lower Washakie, Lower Uinta) may all be regarded as marking the close of the

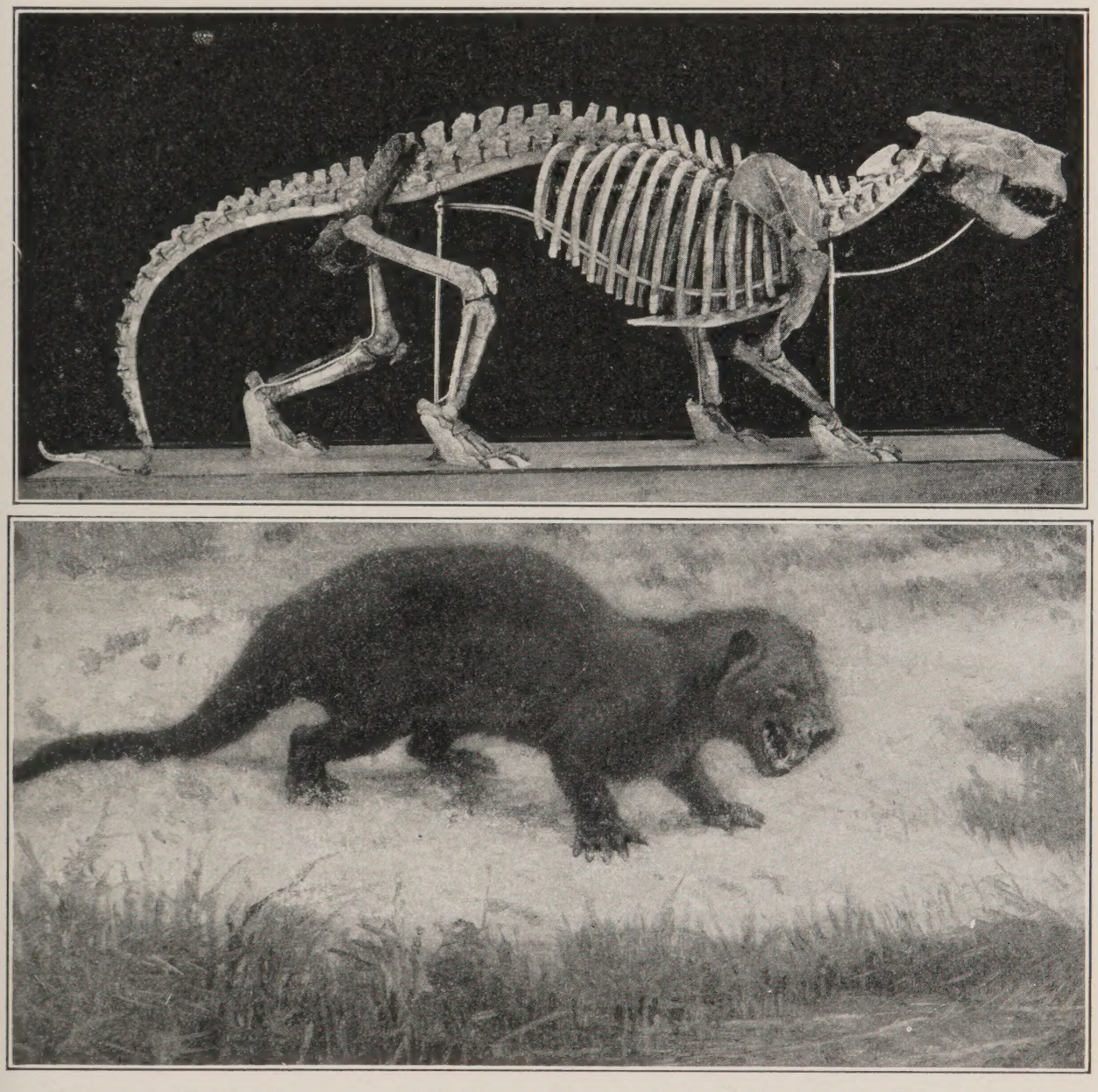


FIG. 65. — *Patriofelis*, a powerful, jaguar-like creodont of the Middle Eocene. Above: Skeleton of *Patriofelix vorax* from the Bridger. Below: Restoration of the same by Charles R. Knight. Both in the American Museum of Natural History.

Middle Eocene, although the distinction between Middle and Upper is naturally a somewhat artificial one and employed for purposes of convenience.

(3) *Lower Uinta: Uintatherium Zone.* — While the Upper Bridger and Lower Washakie deposits were accumulating north of the Uinta Mountains, the base of the Uinta series began to form south of this range, in northeastern Utah. The lowermost beds (Uinta A) are composed largely of

coarse, fluviatile materials and contain but few fossils, including Dinocerata, the rhinoceroses (*Amynodon*), and *Triplopus* (an excessively light-limbed hyracodont), the aberrant titanotheres *Sphenocœlus* and *Metarhinus*. The latter titanothere appears to be a dwarf and possibly aquatic or river-frequenting form, hence the specific name, *M. fluviatilis*.

Upper Eocene, as Represented in the Upper Washakie and Middle and Upper Uinta. The Ludian Stage

Upper Washakie : Eobasileus Zone. — In these famous beds, constituting the Haystack Mountain, or Mammoth Buttes (Fig. 59) of Cope's

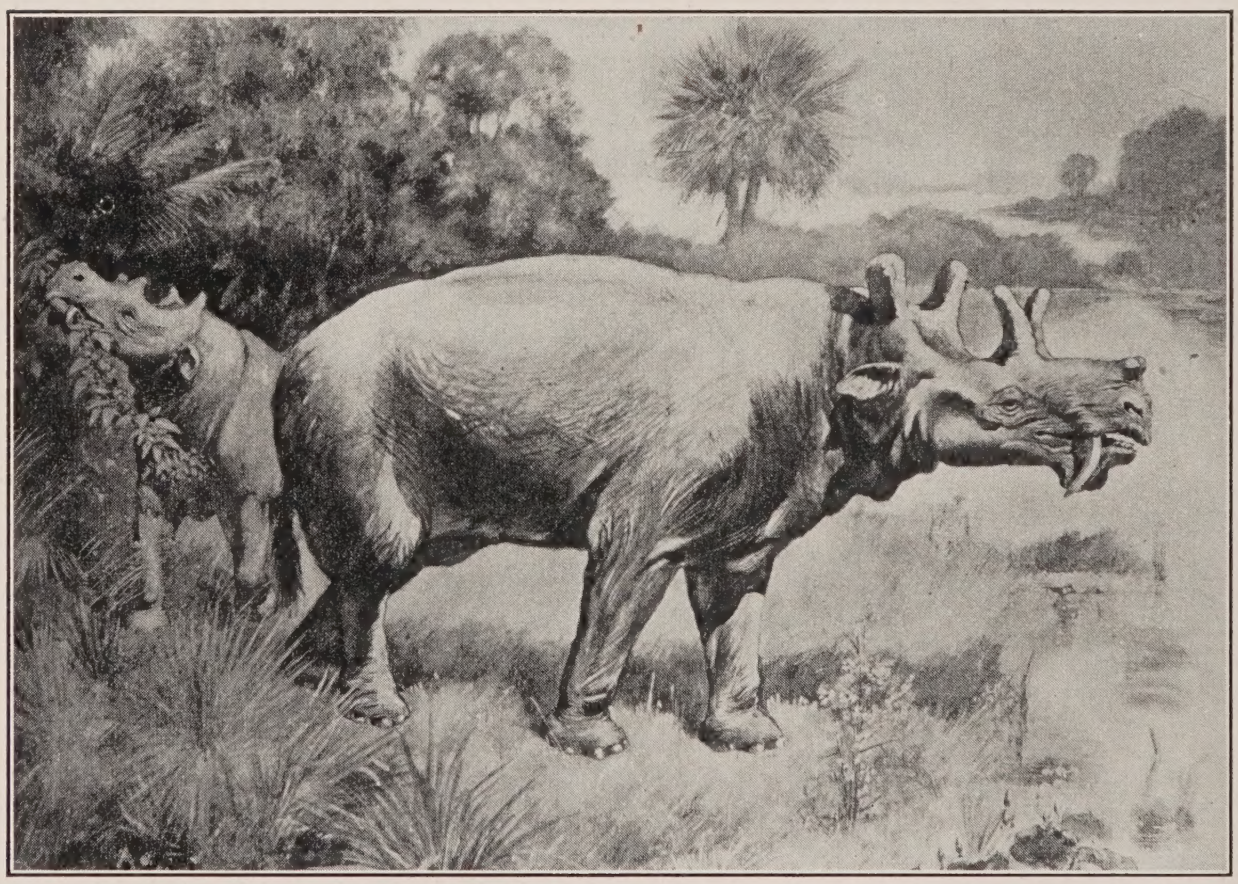


Fig. 66. — The Upper Eocene *Eobasileus*, the four-horned amblypod, last representative of its race. To the left a female, with small horns and tusks ; to the right a male with large horns and tusks. After original by Charles R. Knight in the American Museum of Natural History.

descriptions, the archaic fauna is distinguished by the final evolution of the Amblypoda into giant specialized Dinocerata, including the extremely long-headed form, *Eobasileus* (= '*Loxolophodon*') of Cope.[1] *Eobasileus* (Fig. 66) represents a distinct phylum of amblypods, as shown by the more posterior position of the front pair of horns and the consequent great elongation of the snout; in *Tinoceras* the front horns are more anterior in position, and the snout is thus relatively shorter, the proportions of the

[1] The type of the genus *Tinoceras*, namely, the species *T. anceps* is from the Upper Bridger, Sage Creek, Horizon C. The type of the species *T. ingens* is *probably* from the Lower Washakie. (W. D. M. 1909).

whole being less dolichocephalic. Another feature of the archaic fauna is the giant size attained by members of the creodont mesonychids, the skulls of which equal those of the large modern brown bears of Alaska. The oxyænids are represented by much larger and more specialized forms of *Limnocyon* than those from the Upper Bridger.

In regard to the modernized fauna the most conspicuous fact is the first appearance among the Perissodactyla of a new family of rhinoceroses, destined to become amphibious (Amynodontidæ). Among titanotheres the extremely brachycephalic *Palæosyops*, belonging to a phylum already dwarfed (*P. copei*) in the lower stage, is now apparently extinct. The

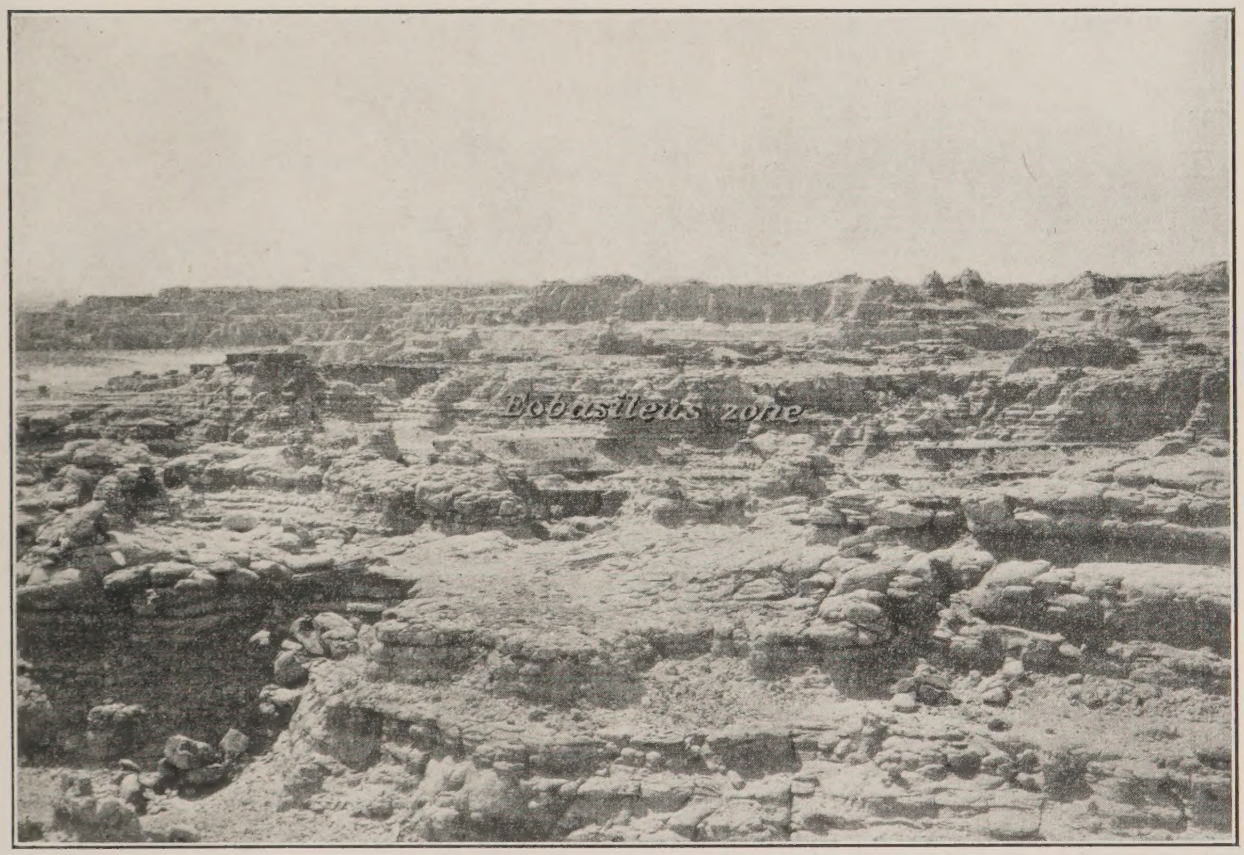


FIG. 67. — Heart of the Washakie Badlands in the Eobasileus Zone, "Adobe Town," five miles east of Kinney Ranch, Wyoming. Photograph by American Museum of Natural History, 1895.

most signal advance in this titanothere family is the appearance of the extremely long-headed *Dolichorhinus* (Fig. 49) with incipient horns, an extreme type also destined to become extinct, while the less extreme prophet-horned titanothere *Manteoceras* (Fig. 49) apparently survives and gives rise to certain of the giant quadrupeds of the Lower Oligocene. Among Artiodactyla of the entelodont family the robust 'giant pig' or omnivore *Achænodon* is also distinctive of this level. The other mammals represent a continuation of the Bridger fauna. All the small mammals are comparatively rare, probably because the coarse conditions of deposition were unfavorable for their preservation. Thus the Equidæ and the Artiodactyla of this stage are still unknown. The mammals characteristic of this deposit

(*Dolichorhinus*, *Amynodon*, and *?Eobasileus*) are also found in the Middle Uinta, south of the Uinta Mountains; several other genera are common to these two formations.

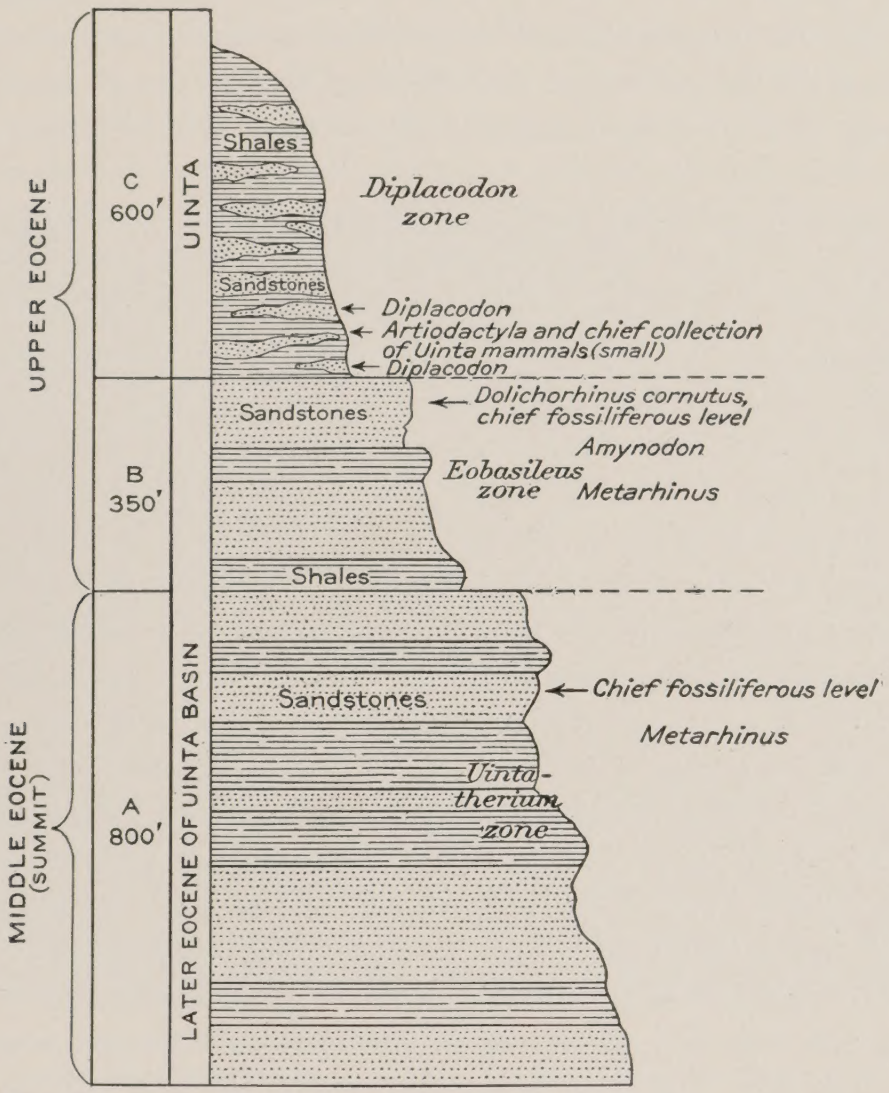
Middle Uinta: ?Eobasileus Zone. — This level is believed to be of the same age as the Upper Washakie because of the presence of a great abundance of the long-skulled titanothere *Dolichorhinus* of the species *D. hyognathus*. Other titanotheres abundant here are of the supposed fluviatile or *Metarhinus* type. Among rhinoceroses, two phyla, namely, the light-limbed

FIG. 68. — Upper Eocene Uinta Formation, near the mouth of White River, Utah. Base of Uinta, Horizon C. The true Diplacodon Zone. Wortman and Peterson prospecting. Photograph by American Museum of Natural History, 1895.

hyracodonts (*Triplopus*) and the amynodonts (Fig. 75) occur. These amynodont rhinoceroses are distinguished by powerfully developed upper and lower canine teeth; they now considerably exceed the existing tapirs in size. This geological level is also distinguished as containing limb bones of the last known survivors of the great Amblypoda, but these animals have not as yet been specifically determined. Another distinguishing feature is that the Artiodactyla are more numerous and varied because it is at this stage that we first know of the existence in America of the very important family of Hypertragulidæ (*Leptotragulus*, *Leptoreodon*), small selenodont ruminants which were at one time believed to be ancestral to the camels and oreodonts, but are now considered (Matthew) distinct. The entelodonts are represented by *Protelotherium*, a successor of *Achænodon*. Among the unguiculates, two families of rodents are recorded: (1) Ischyromyidæ (*Paramys*), and (2) Heteromyidæ (*Protoptychus*). Of the archaic Carnivora the oxyænids and mesonychids still survive, the latter family being represented by the giant form *Harpagolestes*, which is also

recorded in the Upper Washakie. Among the modernized or progressive Carnivora the first true dogs (Canidæ) are reported here (*Procynodictis*). Altogether these beds closely agree with the Upper Washakie, and together may be considered as constituting the base of the Upper Eocene.

Upper Uinta: Diplacodon Zone. — These upper or true Uinta beds were named by Marsh [1] in 1877 as the site of an important stage in the



By permission of the U.S. Geological Survey.

FIG. 69. — Scale section of the Middle and Upper Eocene of the Uinta Basin. After Peterson.

evolution of the titanotheres, the genus *Diplacodon*. Here too is found a robust titanothere known as *Protitanotherium*, which is intermediate between *Manteoceras* and the horned titanotheres of the Lower Oligocene; in this animal the horns are prominent, oval, osseous projections at the junction of the frontal and nasal bones. Altogether three or four phyla of titanotheres occur here, including animals equal in size to the largest existing rhinoceroses. Thus it would appear that after the extinction of the Dinocerata the titanotheres at once became the dominant quadrupeds of

[1] Marsh, Introduction and Succession of Vertebrate Life in America. *Amer. Jour. Sci.*, ser. 3, Vol. IX, 1877, pp. 337–378.

western America. The Equidæ are represented by *Epihippus*, the very diminutive horse in a stage of evolution which is not quite so advanced as that of *Lophiotherium cervulum* of the *gypse*, or Ludian, stage of France. The tapirs (*Isectolophus*) and rhinoceroses (*Amynodon*) occur, but in general we observe that forest and fluviatile, or river-frequenting, forms are rare in this formation. This explains perhaps why the bunodont or omnivorous entelodonts, or elotheres, have not been found. The conclusion is that the conditions of deposition and fossilization at this time were less favorable to the collection of river and swamp dwellers, and more favorable to the preservation of the upland and meadow or field Herbivora.

For the first time in North American history the Artiodactyla of the ruminant division, or Pecora, begin to abound, herbivores of diminutive and intermediate size, with short-crowned molar teeth of the crescentic or selenodont pattern. The Dichobunidæ, or Homacodontidæ, are represented by *Bunomeryx*. Most interesting is the rise of the camel family. Thus the Camelidæ, or Hypertragulidæ, are represented by four genera, *Leptotragulus*, *Protylopus*, *Camelomeryx*, *Oromeryx*. Of these, the diminutive *Protylopus* has been selected as the possible ancestor of the grand phylum of American camels. The polyphyletic tendency in this family is already displayed, and undoubtedly more than one line is represented here. The Oreodontidæ are similarly abundant, embracing ancestors both of the typical oreodonts (*Protoreodon*) and of the aberrant agriochœrids (*Protagriochœrus*).

Among the carnivorous enemies of these Herbivora were the smaller creodont oxyænids and the giant *Mesonyx*, as well as the smaller fox-like canids or pro-Carnivora, *Miacis* and *Procynodictis*. This is the last appearance in North America of these two creodont families (Oxyænidæ and Mesonychidæ), and there is some reason for thinking that the American Hyænodontidæ (*Sinopa*) had already become extinct and that the hyænodonts which we shall find appearing in the Lower Oligocene were invading forms from the Old World or from the north. If this proves to be the case, it may be said that the Upper Eocene of America is marked by the final disappearance of all the archaic herbivorous and carnivorous mammals of American residence as well as by the incipient extension of the great order Artiodactyla.

The Atlantic Coast Region

The Zeuglodon Zone. — The Zeuglodon Beds of the southeastern states are referred to the Jackson [1] Formation, which is regarded as the middle

[1] Lyell, 1847, was the first to assign the Zeuglodon beds to the Jackson Formation below the Vicksburg; this was recognized by Hale, and strongly insisted on by Hilgard (1867). The Jackson was regarded by Dana (1895) as Middle Eocene, approximately equivalent to the Bridger Formation in the Rocky Mountain region.

or the summit of the Eocene. As described by Schuchert and Lucas,[1] the beds vary in thickness from five to ten feet, but are of great geographic extent, since bones are recorded from Florida to Arkansas. In Choctaw County, Alabama, the strata are buff or whitish marl with some green glauconitic sand. They thus belong to an old soft seabottom, in which the bones are either isolated, or more or less of a skeleton may be found in position and undisturbed.

The great marine mammal known as *Zeuglodon* undoubtedly lived in large numbers in the ancient Gulf of Mexico, as well as in the seas of southern Europe and northern Africa. Its proportions were not like those of

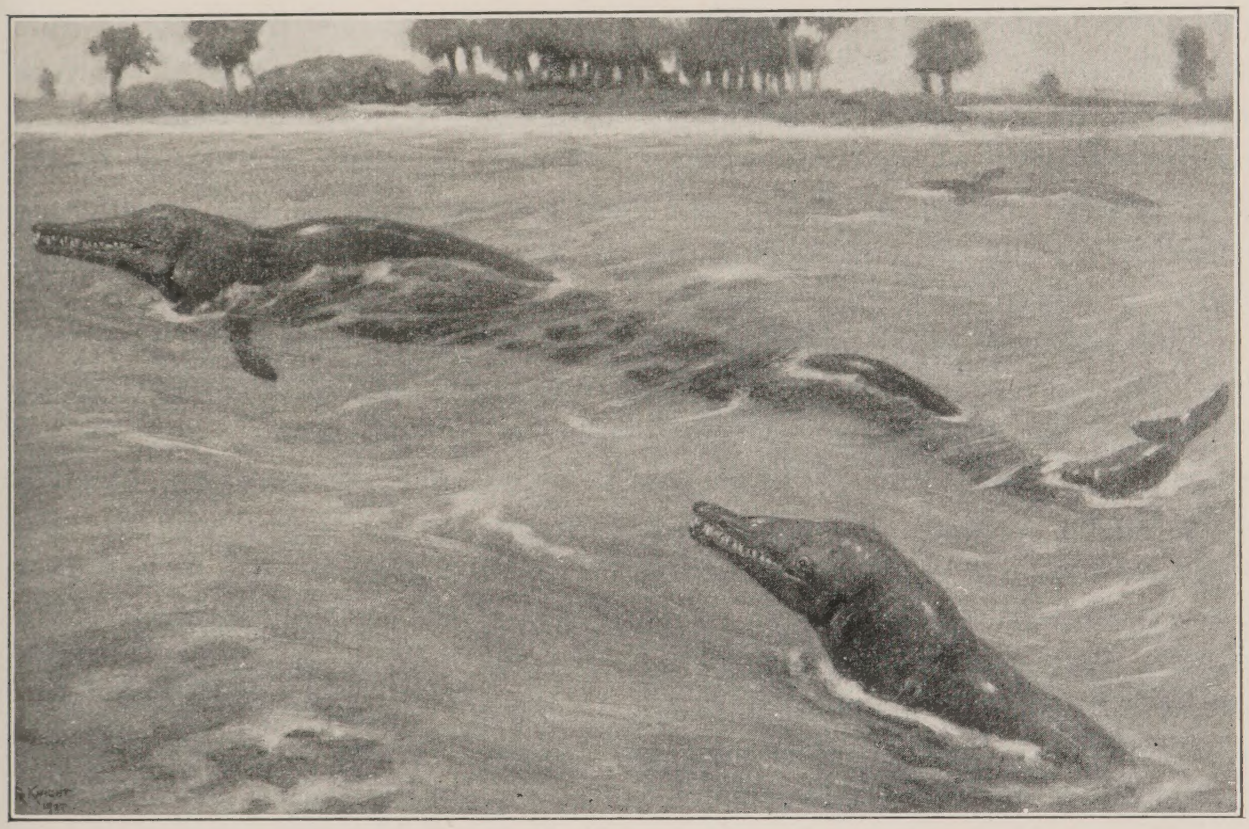


FIG. 70. — The primitive whale *Zeuglodon cetoides* from the Eocene of Alabama. Drawn by Charles R. Knight under the direction of F. A. Lucas. Original in the American Museum of Natural History.

the existing whales, because the diameter was not more than six or eight feet through the thickest part of the body, while the length reached fifty or even seventy feet, about forty feet of which constituted the long and freely movable tail. This tail, in the opinion of Lucas,[2] ended in a fluke, which would indicate that the mammal was a constant diver. The head was relatively small, but the jaws were provided with great grasping and cutting teeth. There was a pair of short fore paddles just behind the head, but the hind limbs were vestigial and retained within the skin. The shoulder blades were like those of a whale, but the extremely elongate

[1] Lucas, F. A., The Pelvic Girdle of Zeuglodon, *Basilosaurus Cetoides* (Owen), with Notes on Other Portions of the Skeleton. *Proc. U.S. Nat. Mus.*, Vol. XXIII, pp. 327–331, 1900.

[2] Lucas, Animals of the Past. New York, 1901.

vertebræ differ from those of any other known animal. The ancestral zeuglodonts are known in the Eocene of Africa. It appears possible that these great American forms are migrants from the Mediterranean seas of the Old World (see p. 73).

Causes of Extinction of the Archaic Orders of Eocene Mammalia[1]

Extinction is not on the same scale nor due to the same causes throughout the successive geologic epochs. The great law of mammalian improvement through the elimination of the least fitted becomes less sweeping in its effects as time goes on and the Mammalia become perfected. Eocene extinction is chiefly that of whole *orders* of archaic mammals. Late Eocene and Oligocene extinction is preëminently that of inadaptive *families*. Miocene times complete the elimination of families and are characterized by the extinction of inadaptive *genera*. This is also true of Pliocene times. The especial feature of Pleistocene times is the ruthless and world-wide extinction of highly adaptive kinds of mammals in certain parts of the world, both of *genera* and of *species*.

Competition of lower and higher types. — It is a very striking fact that not only the archaic but a very large proportion of what we may term the prophetic, modernized, Eocene mammals became extinct at or before the close of this period. The causes of extinction were probably not the same in the two groups. The archaic mammals are very generally distinguished by extremely small brains. This is certainly true of many of the creodonts, of *Phenacodus*, *Coryphodon*, and the Dinocerata. This limited brain power placed these quadrupeds at a disadvantage in competition with the higher placentals. Under contemporary or prevailing conditions of life, intelligence and instinct are matters of first importance in relation to quickness, alertness, adaptability to new conditions. Modern quadrupeds differ widely in this regard; on the western plains of North America, for example, the horses by their resourcefulness save their lives where cattle perish. The cursorial Phenacodontidæ measured their psychic powers with the cursorial Equidæ; the tooth structure in the two families was substantially the same, but the phenacodonts were handicapped by a lower brain organization and by an inferior foot mechanism. The long survival and steady increase in size of the clumsy Amblypoda is one of the most astonishing phenomena of Eocene mammal life. The extinction of these mammals may be attributed to two causes: the low brain power, which may have inhibited the proper defense and care of the young, and the arrested evolution of the grinding teeth, which are actually no larger and little more effective for the comminution of food in the giant *Uintatherium* than in the smaller *Coryphodon*. It is noteworthy that where the

[1] Osborn, H. F., The Causes of Extinction of Mammalia. *Amer. Natural.*, Vol. XL, no. 479, Nov. 1906, no. 480, Dec. 1906. *See especially* pp. 856–857, 850–854, 842.

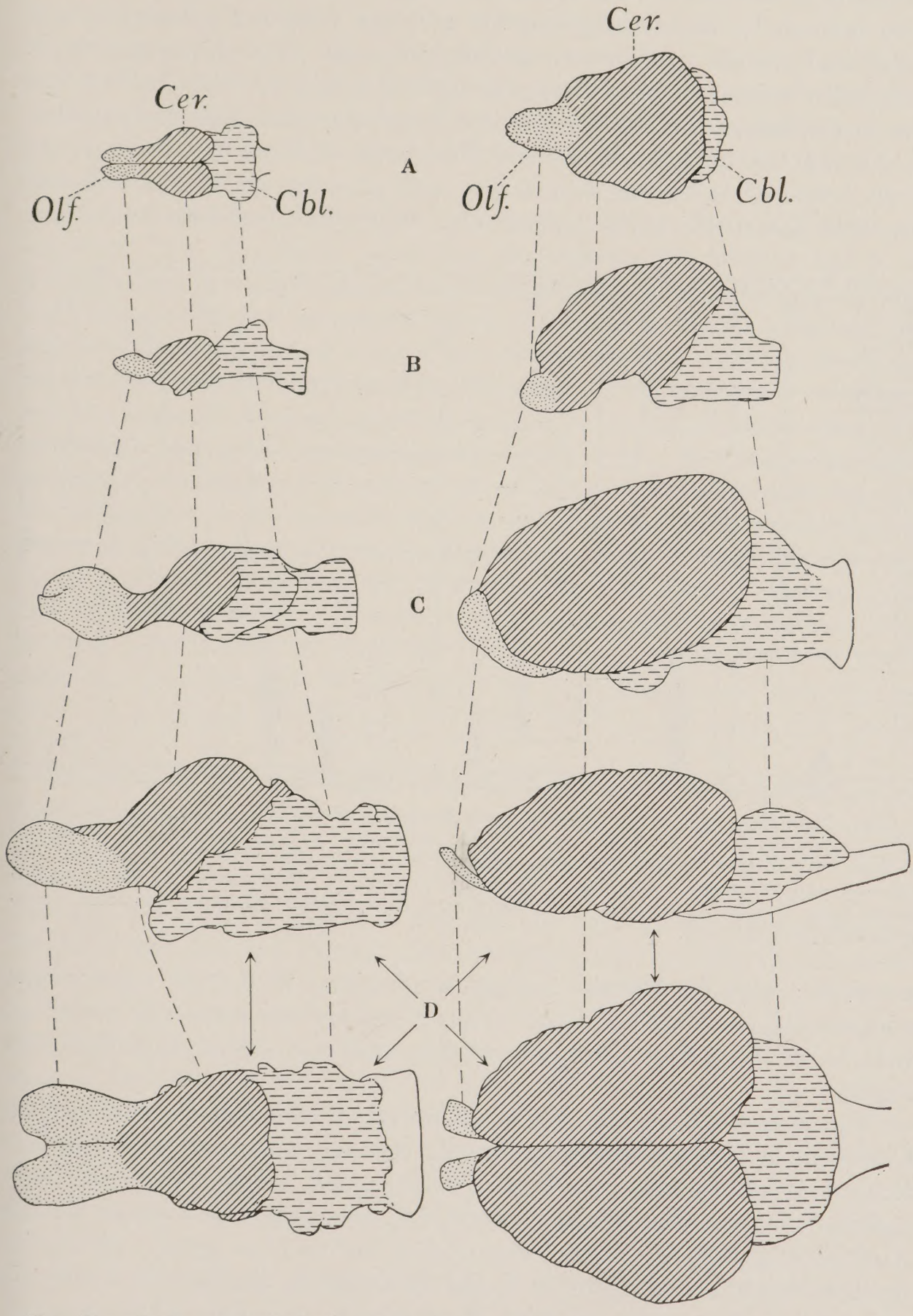


FIG. 71. — Brain proportions in archaic (left) and modern (right) mammals of similar size. Olfactory lobes (dots), cerebral hemispheres (oblique lines), cerebellum and medulla (dashes).

Arctocyon A *Canis*
Phenacodus B *Sus* (Domestic)
Coryphodon C *Rhinoceros*
Uintatherium D *Hippopotamus*.

evolution of an animal runs to the development of tusks and horns, probably favored by sexual selection, the grinding teeth are apparently neglected and are apt to show arrested development. The widespread belief that bulky animals tend to disappear first is inconsistent with the fact that the small phenacodonts became extinct long before the large Amblypoda.

Among the modernized Eocene Herbivora of Europe, several of the small Artiodactyla became extinct very soon after the period which marked the extinction of the bulky lophiodonts. Thus bulk is chiefly fatal where

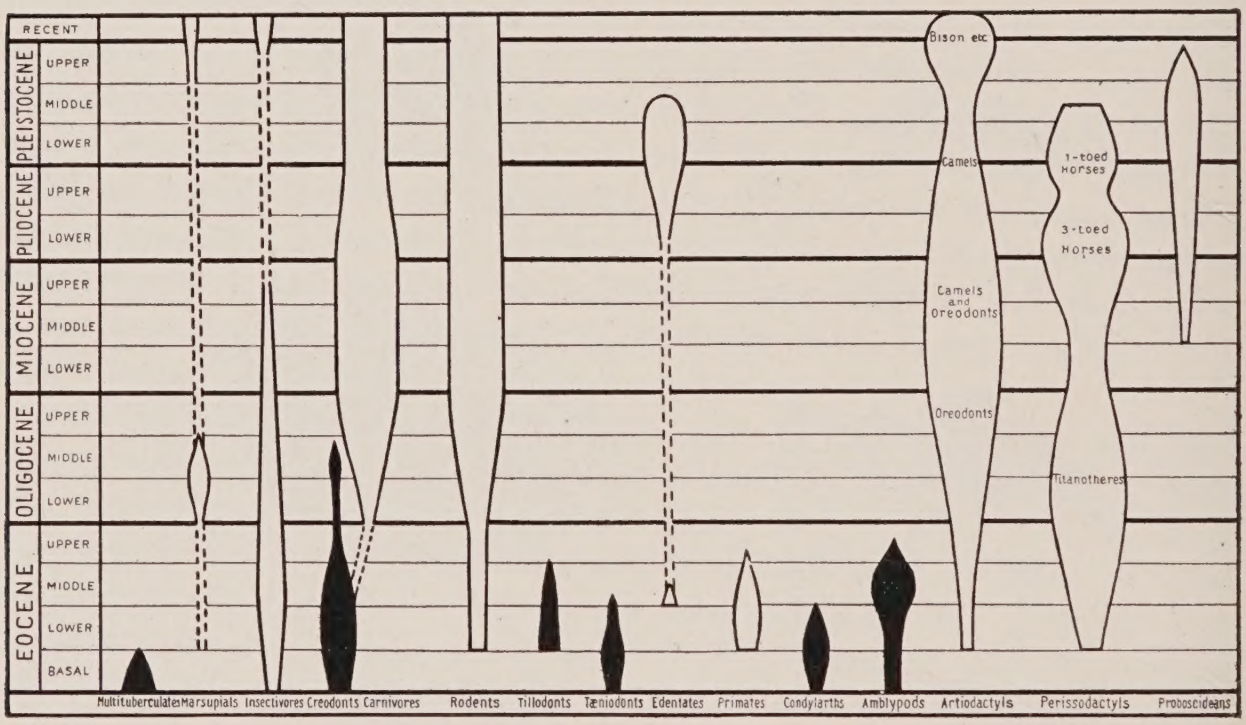


FIG. 72. — Evolution of mammals in North America. (In solid black) Archaic mammals which became extinct in the Eocene and (creodonts) Oligocene Epochs, namely : multituberculates, creodonts, tillodonts, tæniodonts, condylarths, and amblypods. (In hollow lines) Appearance and extinction of archaic and modernized mammals which survive to Pleistocene or recent time, namely : marsupials, insectivores, carnivores, rodents, edentates, primates, perissodactyls, proboscideans.

correlated with inadequate feeding mechanism, with brain power not adequate to enabling the females to defend and care for the young as well as to meet new conditions of life, and with inadequate defensive organs.

The competition of the archaic Creodonta with the diminutive pro-Carnivora in Eocene times may be only remotely compared to the extinction of the Tasmanian wolf (*Thylacinus*) and Tasmanian devil (*Sarcophilus*) through the introduction of the true dog (*Canis dingo*) on the Australian main land.

The steady increase in size of the creodonts as displayed in *Patriofelis* and in the enormously powerful *Harpagolestes* is a fact which may be placed parallel with the increasing size of the Amblypoda.

It is noteworthy that the only archaic Carnivora which persisted into the Lower Oligocene are the hyænodonts, in which the brain actually in-

creased in size. Marsh's laws [1] of the relations of brain growth to survival are apparently borne out by these comparisons, namely, that the brains of surviving races are upon the average larger than those of declining races. On the other hand in following the many causes of extinction through the entire Cænozoic we shall find that even large cerebral development, as in certain rhinoceroses (*Teleoceras*) and elephants (*Mastodon*), may fail to preserve a race.

Diminished or contracted land areas. — In Europe especially the varying coast lines, the insular conditions, the archipelagic surfaces, are to be seriously studied in connection with the extinction which overtook so many characteristic Eocene mammals before the opening of the Oligocene, so that the general aspect of the fauna is altogether different when the Oligocene fairly opens. Changes of land caused by elevation or subsidence operate indirectly through causing changes in all the physical conditions of climate, moisture, desiccation, temperature, and so forth; also more directly in facilitating the cutting off of migrations and introducing new competitions. North America and Africa were the stable continents of Tertiary times, which underwent slight fluctuations of land area as compared with the highly unstable continents of Europe and the southern half of South America. It must be stated, however, that the main phenomena of extinction in unstable Europe coincide with those in stable America. We have seen in group after group that the Upper Eocene mammals of peninsular Europe are not those which in the main give rise to the Oligocene fauna.

A glance at western North America in Tertiary times as studied by J. Perrin Smith [2] displays the important influence which must have been exerted by the relations of the Arctic, Pacific, and Atlantic oceans as affected by continental elevation and depression. During part of the Cretaceous, Smith believes that Asia and the Alaskan peninsula were connected across Behring Straits. Whenever the cold currents of the Arctic Ocean were cut off, the western coast of America enjoyed a warm, probably a subtropical climate (see p. 93). The same author believes that during early Tertiary times a connection existed between the Eocene seas of the Atlantic and Pacific to the south of California. By Miocene times this passage appears to have been closed. The opinion of this author is based upon the marine fauna. That based upon the land fauna is cited elsewhere (p. 81). In the north the land appears to have risen again toward the end of the Miocene, cutting off the Arctic Ocean, and giving a temperate though not tropical climate to the entire North Pacific.

Insular conditions. — The substitution of *insular* for *continental* condi-

[1] Marsh, Small Size of the Brain in Tertiary Mammals. *Amer. Jour. Sci.*, Vol. VIII, 1874, pp. 66–67; also, On the Size of the Brain in Extinct Animals, Abstr. *Nature*, Vol. XXXII, London, 1885, p. 562.

[2] Smith, J. P., Periodic Migrations between the Asiatic and the American Coasts of the Pacific Ocean. *Amer. Jour. Sci.*, Vol. XVII, Mar. 1904, pp. 217–233.

tions by subsidence has undoubtedly been a potent cause both of extermination in certain localities and of the survival of very primitive forms. It may be said at once that most of the causes both of survival and of extinction which prevail upon continents are intensified on islands.[1] Wallace attributed the widespread extinction which occurred in Australia in early Pleistocene times partly to the increased competition and struggle for existence caused by the progressively contracted land area due to subsidence.[2] Wallace also rightly attributed the survival of certain primitive mammals among the monotremes and marsupials to the practically insular condition of the Australian region. On the other hand, there is reason to believe that the introduction of new forms of life on islands causes more rapid and profound modifications in the fauna than similar introductions on continents.

[1] Osborn, H. F., The Causes of Extinction of Mammalia, *Amer. Natural.*, Vol. XL, no. 479, Nov., 1906, pp. 769–795; no. 480, Dec., 1906, pp. 829–859. (See especially pp. 773–774.)

[2] Wallace, A. R., The Geographical Distribution of Animals (1876). Vol. I, pp. 158–159.

CHAPTER III

THE OLIGOCENE OF EUROPE, NORTH AFRICA, AND NORTH AMERICA

THIS period is sharply defined by great geographic revolutions as well as great transformations in its animal and plant life. In Europe it opens with the main elevation of the Pyrenees and is marked toward the close by the initial elevation of the Alps (Fig. 13, p. 59). We are able to study the Mammalia over a still wider geographic range. In America the principal

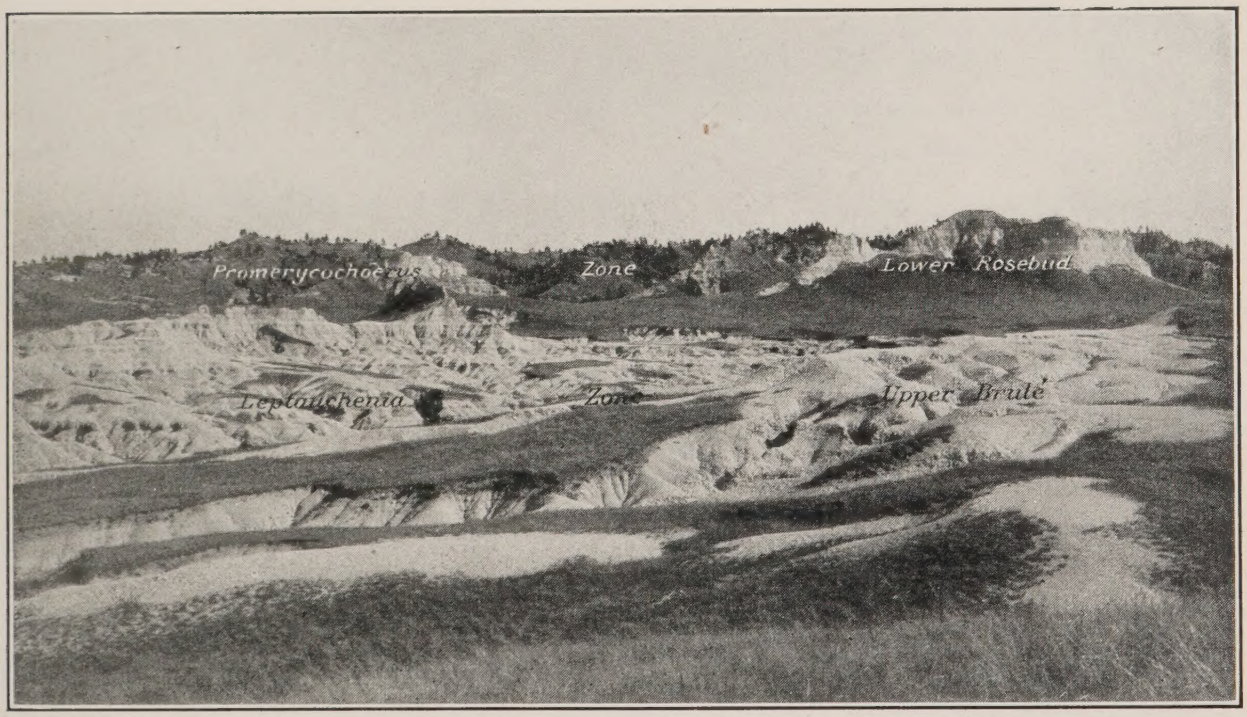


FIG. 73. — Summit of the Oligocene or transition to the Miocene. Lower: Brule Clays, or Leptauchenia Zone. Upper: Lower Rosebud, or Promerycochœrus Zone. Exposures on the south side of the White River, near Porcupine Creek. Photograph by American Museum of Natural History, 1906.

interest centers around our first knowledge of the life of the Great Plains region, a vista we have not enjoyed previously because all our former studies have been confined to the mammals of the mountain region. In Europe the plains fauna still remains unknown.

The most remarkable fact is the remingling by intermigration and by fresh invasions of similar types from the north of the mammals of the New and Old Worlds, so that Europe and western America again constitute a single zoölogical region, or *Holarctica*. We thus enter the FOURTH FAUNAL PHASE.

IV. LOWER OLIGOCENE, FOURTH FAUNAL PHASE—THE SECOND MODERNIZATION. SUDDEN APPEARANCE IN EUROPE AND NORTH AMERICA OF NUMEROUS EXISTING FAMILIES OF MAMMALS. REUNION OF THE NEW AND OLD WORLD INTO A SINGLE ZOÖLOGICAL REGION, FOLLOWED BY ANOTHER LONG PERIOD OF INDEPENDENT EVOLUTION AND PARTIAL EXTINCTION.

The first impression of this phase is our sudden introduction to a large number of modernized types which had been slowly evolving elsewhere, probably in the plains of America and Eurasia. In North America this second modernization is shown to be still more remarkable than the first

Titanotherium zone "White River Group"
"Bridger" and "Uinta" unfossiliferous
Lambdotherium zone "Wind River" banded beds
AMERICAN MUSEUM CAMP

FIG. 74. — Lower Oligocene horizons resting upon the Upper, Middle, and Lower Eocene. Titanotherium Zone = Lower Oligocene. "Bridger" and "Uinta" = Middle and Upper Eocene. Lambdotherium Zone = Lower Eocene. Escarpment of the Beaver Divide, near Hailey, Wyoming. Photograph by American Museum of Natural History, expedition of 1909. Compare Fig. 95.

or Wasatch modernization, which was one of appearance of existing *orders*, because this is one of existing *families*, not as yet recognized in the mountain basins. The Oligocene fauna thus is far more familiar in aspect than the known Eocene. This new list in America includes six existing families of rodents, four existing families of carnivores, one existing family of peris-

sodactyls. A very similar modernization occurs in western Europe, many familiar modern families appearing for the first time.

Several of these new families appear simultaneously in Europe and North America. Thus the two countries which were separated most widely at the close of the Eocene are again brought together in the Lower Oligocene, as shown in the accompanying table.

MAMMALS OF THE LOWER OLIGOCENE

Peculiar to Europe	*Common to Europe and North America*	*Peculiar to North America*
Palæotheres	Titanotheres	Horses
Anoplotheres	Chalicotheres	Hyracodonts (rhinoceroses)
Cænotheres	Rhinoceroses (aceratheres and diceratheres)	Oreodonts
Gelocids	Amynodonts	Camelids
Amphicyonids	Anthracotheres	Hypertragulids
Viverrids	Suillines	Leptictids
Cricetines (hamsters)	Entelodonts	Chrysochlorids? (insectivores)
Theridomyids	Opossums	Ischyromids [1] (rodents)
Sirenians (*Halitherium*)	Hyænodonts	Leporids or hares
	Canids (dogs)	
	Mustelids (martens)	
	Machærodonts (saber-tooth cats)	

The closest correspondence of the Old and New Worlds is seen to be among the perissodactyl ungulates and the carnivores; the least community is among the artiodactyl ungulates, which exhibit fewer families in common. It is a very striking fact that there was little interchange of the artiodactyls of the New and Old Worlds until the Pleistocene.

We note that forest and browsing quadrupeds prevail in both countries. A contrast is the apparent disappearance of the horses in western Europe, and the rapid evolution of these animals in western North America. The continental influence of North America is still displayed in the presence of giant quadrupeds, especially the titanotheres and entelodonts, which greatly surpass in proportions the largest of European mammals of the time, which are of intermediate and smaller size; there is also, on the whole, a greater diversity in the American life. In the two countries six of the great families of perissodactyls and artiodactyls of Eocene origin die out. The last of the archaic carnivores (hyænodonts) survive only to the Middle Oligocene.

[1] The Ischyromyidæ, the American Eocene Rodentia *par excellence*, are regarded by Matthew as a primitive Eocene and Early Oligocene (*Ischyromys*, *Prosciurus*, *Cylindrodon*) group of squirrel-like or sciuromorph rodents. The great masseter muscle of the jaw lies entirely behind the infraorbital foramen, as it does in the existing sewellels (Haplodontidæ), also peculiarly American rodents, first observed in the Upper Oligocene, or John Day, and in the specialized Mylagaulids, a peculiar family of horned rodents of the Upper Miocene, both Sciuromorpha.

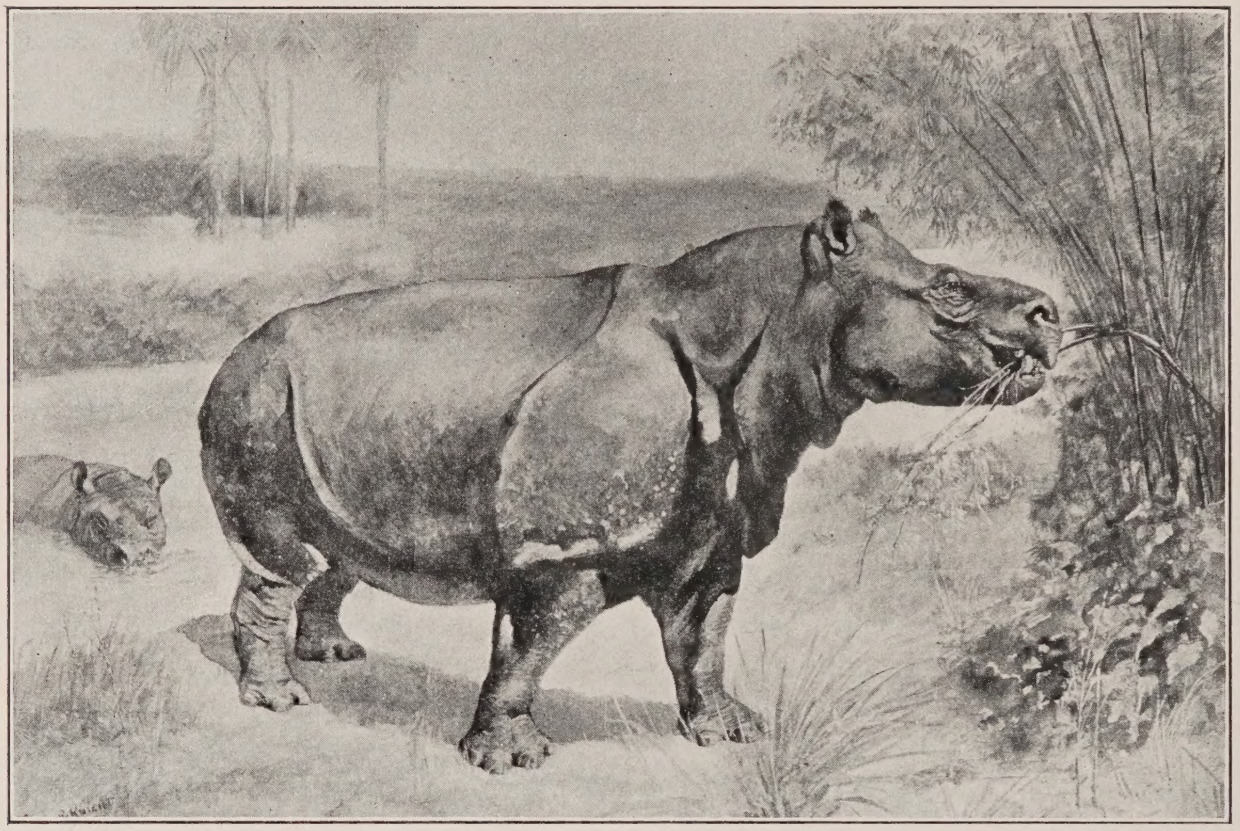


FIG. 75. — Amynodonts, aquatic rhinoceroses of Europe and America. The Lower Oligocene *Metamynodon* of South Dakota. After original by Charles R. Knight in the American Museum of Natural History.

The especially characteristic hoofed mammals, common to this great holarctic region and dominating in the two countries, which attain their maximum evolution and then disappear, are the following:

TYPES	SUPPOSED ORIGIN
Diceratheres, pair-horned rhinoceroses.	North America
Amynodonts, amphibious rhinoceroses with canine tusks	" "
Entelodonts, giant pigs with elongate skulls and stilted limbs	Eurasia
Anthracotheres, buno-selenodont artiodactyls, varied and attaining giant size in Europe only.	"

These animals are all descendants of Upper Eocene ancestors. Among artiodactyl ungulates we discover partly descendants of Eocene families, partly new invading forms, the latter especially seen in Europe. The prevailing artiodactyls common to both countries exhibit five-cusped, brachyodont, buno-selenodont molar teeth (anthracotheres); bunodont teeth are more rare (suillines and entelodonts). True four-cusped selenodont molars of modern type are observed in the oreodonts and hypertragulids and, in more specialized form, in the smaller pro-ruminants, or gelocids, newly arriving; also in the true ruminants, or cervulines, arriving in Europe in the Middle Oligocene, both probably of south Asiatic origin. It is noteworthy that all these primitive Oligocene ruminants of Europe, like their selenodont contemporaries, the hypertragulids in America, are *hornless* but usually provided with defensive tusks.

The cænotheres are especially characteristic of the European Oligocene, although a few traces of the family appear as early as the *Ludian* (Upper Eocene). The cænotheres and surviving dichobunes of Europe, in spite of certain resemblances in their tooth structure, are very remote from one another; in fact, the cænotheres form a somewhat isolated group (see p. 548). These peculiarly European forms reached their culmination in the Middle Oligocene, declined before the Oligocene ended, and seem to have become entirely extinct soon after the appearance of the invaders of the Miocene.[1]

FIG. 76. — Entelodonts, giant pigs of Europe and America. A Middle Oligocene stage. (The position of the ears in this restoration is erroneous; they are placed too high. See Fig. 83.) After original by Charles R. Knight in the American Museum of Natural History.

In America the majority of the Oligocene mammals have been discovered in the single geographic region of Dakota and in a continuous series of depositions not exceeding 600 feet in thickness, which are known as the White River Group. Similar forms have been found in Wyoming, Montana, Colorado, and British Columbia. In Europe we find an analogous fauna in beds of very different geologic origin, and interspersed with rich records of plant life which are practically wanting in America.

This is one of the most conspicuous instances of the advantages of correlation. Were it not for the convincing evidence to the contrary afforded by the Old World, we should be inclined to regard the American Oligocene as a period marked by few geographic changes, but by certain

[1] Stehlin, H. G., Die Säugetiere des schweizerischen Eocæns, 1903–1906, pp. 675, 687, 690.

grand evolutionary changes in mammalian life; in other words, it is chiefly the vast evolutionary changes in the American mammals (horses, titanotheres, and rhinoceroses) which enable us to realize the enormous duration and grandeur of Oligocene times in America.

As the Oligocene advances, the countries again diverge and become dissimilar in their faunal aspect. The correlation of the great time divisions and depositions in which these changes occur are as follows:

Life Zones	*European Stages*	*American Formations*
Diceratherium Zone	Aquitanian	Harrison John Day Formations White River (Upper)
Metamynodon (= *Cadurcotherium*) Zone	Stampian	White River (Middle)
Ancodus (*Titanotherium*) Zone	Sannoisian	White River (Base)

Palæogeography

Continental connections. — With the Oligocene began an emergence of the continents from their prolonged Eocene submergence. The land masses of Europe, Asia, and North America became connected.[1] This is the theoretical explanation of the intermigrations which followed and of the invasion of a new fauna into North America and Europe, coming presumably from the circumpolar region. Whether the connection between the Old and New Worlds was by way of Alaska or across the whole breadth of the great polar continent is uncertain. In the accompanying map by Matthew the connection is indicated by way of Alaska and eastern Asia. In general the southern continental masses (South America and Australia) appear to have been disconnected. Of the great Lower Oligocene fauna now known in northern Africa, the larger part is exclusively African in type, but a smaller part includes a few mammals, such as the hyænodonts, anthracotheres, certain suillines, and smaller rodents, which are also known in the Upper Eocene and Lower Oligocene of France.

The fluviatile and estuarine sea-cows, or sirenians, were probably common to all the Mediterranean borders, African, Asiatic, European, and even the western Atlantic in Oligocene times. The Eocene Egyptian types (*Eotherium, Eosiren, Protosiren*) are more primitive in the possession of hind limbs. The earliest of the European forms is *Halitherium* (*H. veronense*) from Middle Eocene limestones of northern Italy (Monte Zuello). The most primitive form in skull and tooth structure is *Prorastomus* from the (?) Eocene of the island of Jamaica, West Indies. The Oligocene stage is *Halitherium schinzi* from marine sands near Basel, Paris, Bordeaux, and Belgium.[2] The fact

[1] De Lapparent, A., Traité de Géologie, 1906, p. 1547.

[2] Abel, O., Die Sirenen der mediterranen Tertiärbildungen Österreichs. *Abh. K. K. Geol. Reichsanst.*, Vol. XIX, no. 2, Vienna, 1904. *See especially* pp. 214–223.

that the Middle Eocene sirenians of Europe are *more* specialized than the Upper Eocene sirenians of Africa might be cited as evidence that the sirenian center of diffusion was likewise to the northward.

Geographic changes in Europe. — The early earth movements of the Oligocene caused an invasion of the sea in the north of France, and in Germany as far south as Leipzig. This vast northern ocean of Tongrian and Stampian age is believed to have made the northern climate of Europe more

FIG. 77. — **Oligocene.** A period of continental elevation and reunion followed by the reëstablishment of connections between the life of the New and Old Worlds. Central Europe submerged or partly archipelagic. African mammals and birds partly similar to those of Europe. Madagascar united with Africa. South America entirely separated, its mammals developing independently. Australia entirely separated. Closing the Oligocene, another long interval of separation between North America and Europe. Rearranged after W. D. Matthew, 1908.

temperate. The lignitic flora of south central Germany now includes sequoias, birches (*Betula*), and palms (*Palmacites*).[1] Southern Europe through the rise of the Pyrenees and Swiss Alps was elevated, and conditions were favorable for continental depositions rich in mammalian life both in southern France and in the south of Germany, as shown in Fig. 79.

In the Aquitanian, or Upper Oligocene stage almost all of Europe had again emerged from the sea; great shallow lakes were scattered over France, Switzerland, Germany, Austria, Italy, and Greece. In southwestern France or Aquitania, from which the stage derives its name, there is a renewed advance of the sea over the land. The freshwater lakes are varied by

[1] De Lapparent, A., Traité de Géologie, 1906, pp. 1547–1549.

lagoons and swamps, with lignitic deposits. The flora indicates an increasing humidity, with moderate and equable warmth. The bird life of central France (Allier) is similar to that bordering certain lakes of the interior of Africa to-day.[1] According to De Lapparent,[2] the Oligocene terminated

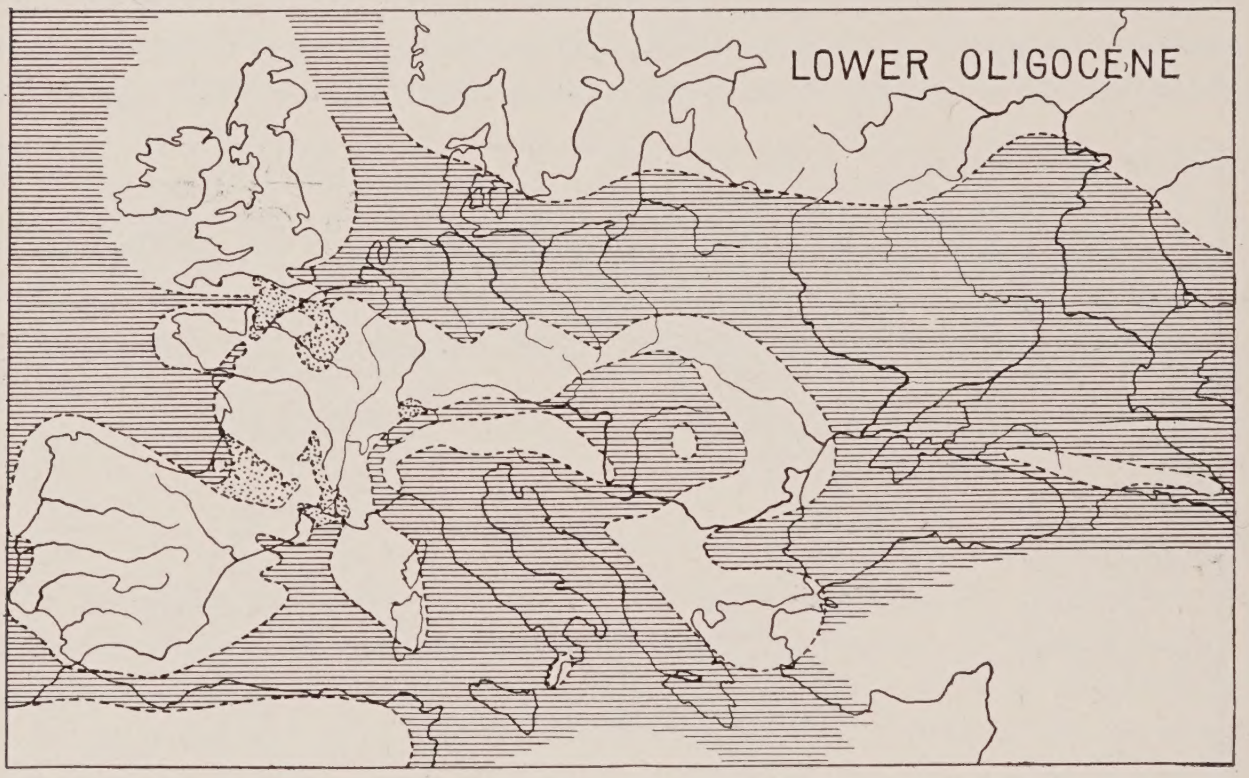


Fig. 78. — Europe in Lower Oligocene or Sannoisian times. White = land. Ruled = sea. Dotted areas = lagoons. After de Lapparent, 1906.

by the drying up of the lakes, deepening of the valleys, and beginning of the river or fluviatile régime of the Lower Miocene. Thus the Oligocene of Europe is physiographically subdivided as follows:

	3. Upper Oligocene.	Aquitanian.	Extensive freshwater lakes and lagoons. Recession of sea.
Tongrian	2. Middle Oligocene.	Stampian.	Advance of sea in Paris Basin.
Tongrian	1. Lower Oligocene.	Sannoisian.	Marine and brackish deposits lacustrine and marine marls.

Flora and Climate

Europe. — A new character is given to the Oligocene flora by the disappearance of many tropical forms, and the appearance of a great many non-tropical forms; with few exceptions this flora has its modern representatives north of the Equator.[3] The temperature fell somewhat, and

[1] Milne Edwards, A., Recherches Anatomiques et Paléontologiques pour servir à l'Histoire des Oiseaux Fossiles de la France. Paris, 1869–1871, p. 570.

[2] De Lapparent, A., Traité de Géologie, 1906, p. 1598.

[3] Schimper und Schenk, Handbuch der Palæontologie, ed. by von Zittel, Pt. II, 1, Palæophytologie, 1890, p. 802.

there was a lessening of humidity. The occurrence of palms (*Sabal, Chamærops*) in the Baltic region indicates a mean annual temperature of at least 18° C. or 64° F., the existing isotherm of southern Spain and Italy. The prevailing forest flora includes palms, sequoias, and numerous other conifers, figs, cinnamons, magnolias, and trees of south temperate forest type. African, Indian, and Australian types become more rare.[1]

Cooler Lower Oligocene conditions of the northern coast of Europe are indicated in the rich flora of the amber beds of Königsberg (55° north), which include pines, spruces, sequoias, cypresses, oaks, chestnuts, beeches, maples, and also the cinnamon; in the main a north temperate flora.[2] The period in general is marked by the increase of conifers and the spread of deciduous trees. Along certain lake borders (Aix, Gargas) of southern France the heat and drought during the latter part of the summer were extreme (de Saporta). The climate of the Oligocene was thus less uniform; the difference in seasons became more marked. We know nothing of the grasses. The structure of the teeth of the mammals indicates the continued prevalence of browsing types, and a very small percentage of grazing and grass-eating types. Forest and swamp-living types are still very numerous. In the Middle Oligocene of central France (Aix) are found conifers, palms (*Flabellaria*), and cinnamons.[3]

North America. —Unfortunately there are no leaf-bearing beds of certain Oligocene age; in fact, we know nothing of the flora of the region of the great plains in Oligocene times. A hint as to the temperature of Dakota is afforded by the discovery by Loomis [4] of crocodiles in the old river deposits of the Lower White River group, sure indication of south temperate or Floridian conditions of climate. The Kenai beds of Alaska, formerly considered Oligocene, are now referred to the Eocene [5] and possibly Upper Cretaceous.[6] Thus we must depend upon Europe for our knowledge of the North American climate, and the presence in the two countries of so many similar forms of mammals indicates a uniformity of temperature.

Physiographic Conditions

Europe. — The abundant localities where Oligocene mammals are found in Europe indicate an undulating country, thickly forested in places, with still-water predominating over fluviatile depositions. In contrast with the Eocene, fluvio-marine deposits are rare. Most localities are 'continental,' or in the interior. Exceptions are the fluvio-marine sands of the Fayûm

[1] Geikie, A., Textbook of Geology. London, 1893, p. 991.

[2] Goeppert, Flora des Bernsteins, Vol. I, 1883, Vol. II (Goeppert, Menge, Conwentz), 1886.

[3] Geikie, A., Textbook of Geology, 1893, p. 990.

[4] Loomis, F. B., Two New River Reptiles from the Titanothere Beds. *Amer. Jour. Sci.*, Dec., 1904, Ser. 4, Vol. XVIII, pp. 427–432.

[5] Knowlton, F. H., Fossil Flora of Alaska. *Bull. Geol. Soc. Amer.*, Vol. V, 1893, p. 587.

[6] Note by Dr. Hollick, March, 1909.

(Fig. 79, 28), on the northern shore of the African continent, and of Hempstead (24). The Upper Oligocene sands of Pyrimont in Savoy (Fig. 84, 4) are of fluviatile origin. The Oligocene opens with the still-water marls and limestones of Ronzon (Fig. 79, 13) in southern France, and closes with the extensive lacustrine or freshwater limestones of St. Gérand-le-Puy (Fig. 84, 2) in the Bourbonnais. Lignites or deposits of thick swamp vegetation are abundant, as at Calaf (Fig. 79, 25) and Tarrega (26), Spain, at Célas (3) (Gard) in France, and Cadibona (Liguria) (Fig. 82, 46) in Italy. Of this period are the fissure deposits or *Bohnerze* of the Jura (Swabia), Frohnstetten (Fig. 79, 17), and other localities. The most famous fissure deposits are those of Quercy (Fig. 79, 12) which, we may recall (p. 151), begin in the Upper Eocene and continue into Middle Oligocene times.

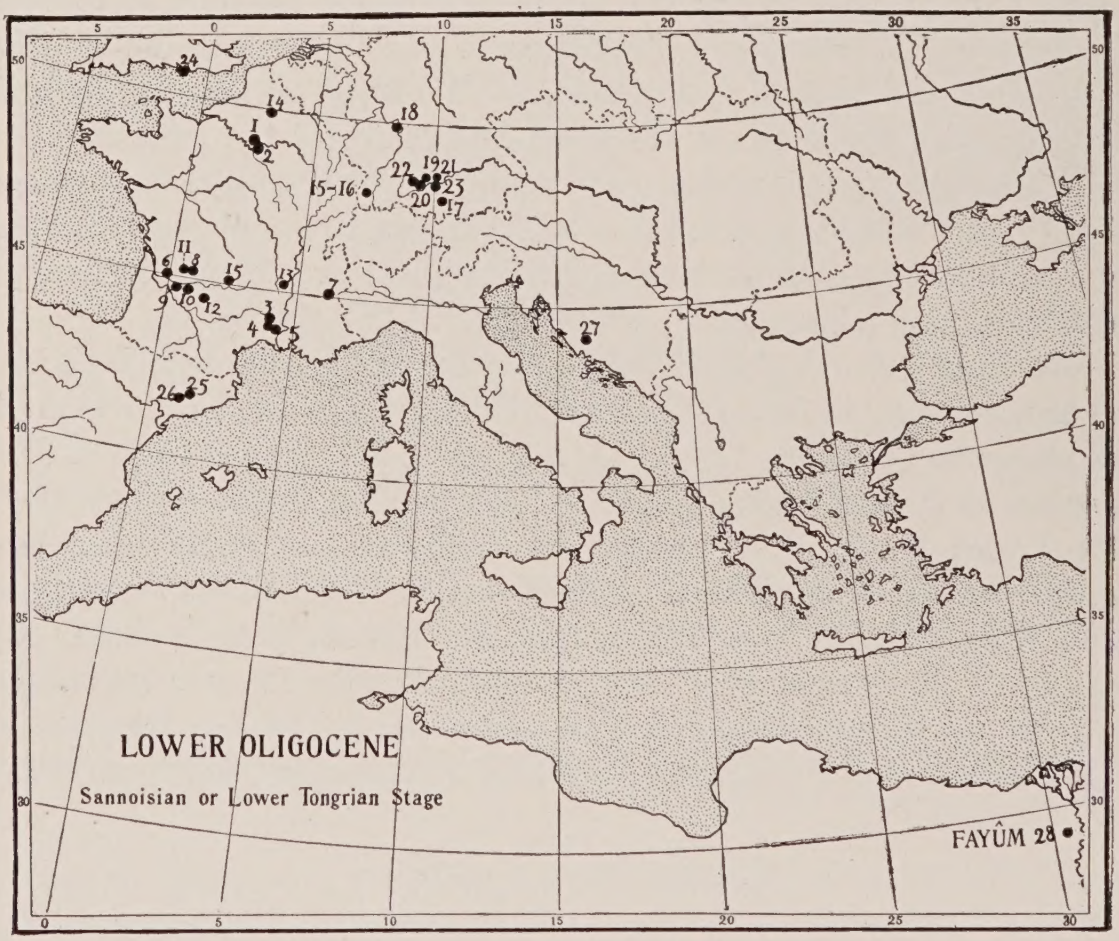


Fig. 79. — **Lower Oligocene.** Sannoisian, or Lower Tongrian. FRANCE. — Lagoon deposits near Paris : marnes blanches de **1** *Pantin*, **2** *Romainville*. Lignites de **3** *Célas*, **4** *Avéjan*, **5** *Vermeil* (Gard). **6** *Fronsac* (Gironde). Calcaire grossier de **7** *La Grave* (Gironde) distinct from that of Paris. Gypse de **8** *Sainte-Sabine* (Dordogne). Argiles de **9** *Duras* (Dordogne). Calcaire d' **10** *Issigeac* (Dordogne). **11** *Saint-Cernin* (Dordogne). Phosphorites du **12** *Quercy*, south central France, in part. Marnes et calcaires (100 meters) de **13** *Ronzon*, near Lyons. Calcaire de **14** *Brie*, north of Paris. GERMANY. — Fluviatile, Melanienkalke von **15** *Brunnstatt*, **16** *Rixheim* (Alsatia). Bohnerz von **17** *Frohnstetten* (Suabia) ; Asphaltkalk von **18** *Lobsann* (Alsatia) ; Bohnerz von **19** *Vehringerdorf*, **20** *Vehringen*, **21** *Eselsberg*, near Ulm, **22** *Hochberg* in Suabian Jura ; Bohnerz von **23** *Oerlingerthal*, near Ulm. ENGLAND. — Fluvio-marine clay and marl (140 ft.) of **24** *Hempstead* on Isle of Wight. SPAIN. — Lignites of **25** *Calaf*, **26** *Tarrega* near Barcelona. AUSTRIA-HUNGARY. — Flysch, freshwater and marine of **27** *Monte-Promina* (Dalmatia). EGYPT. — Sand and clay, fluvio-marine, of **28** the *Fayûm*. Correlation of Depéret.

I. OLIGOCENE LIFE OF EUROPE

Lower Oligocene, Sannoisian, or Lower Tongrian

This stage takes its name from the *marnes de Sannois* in France and from Tongres in Belgium. According to Depéret [1] the early fauna of the *lignites de Célas, Avéjan, Vermeil* (Fig. 79, 3–5), as well as several deposits in the south of France (6–11), part of Quercy (12), and Frohnstetten in Swabia (17) are of this age. The mammals of these deposits do not present any Oligo-

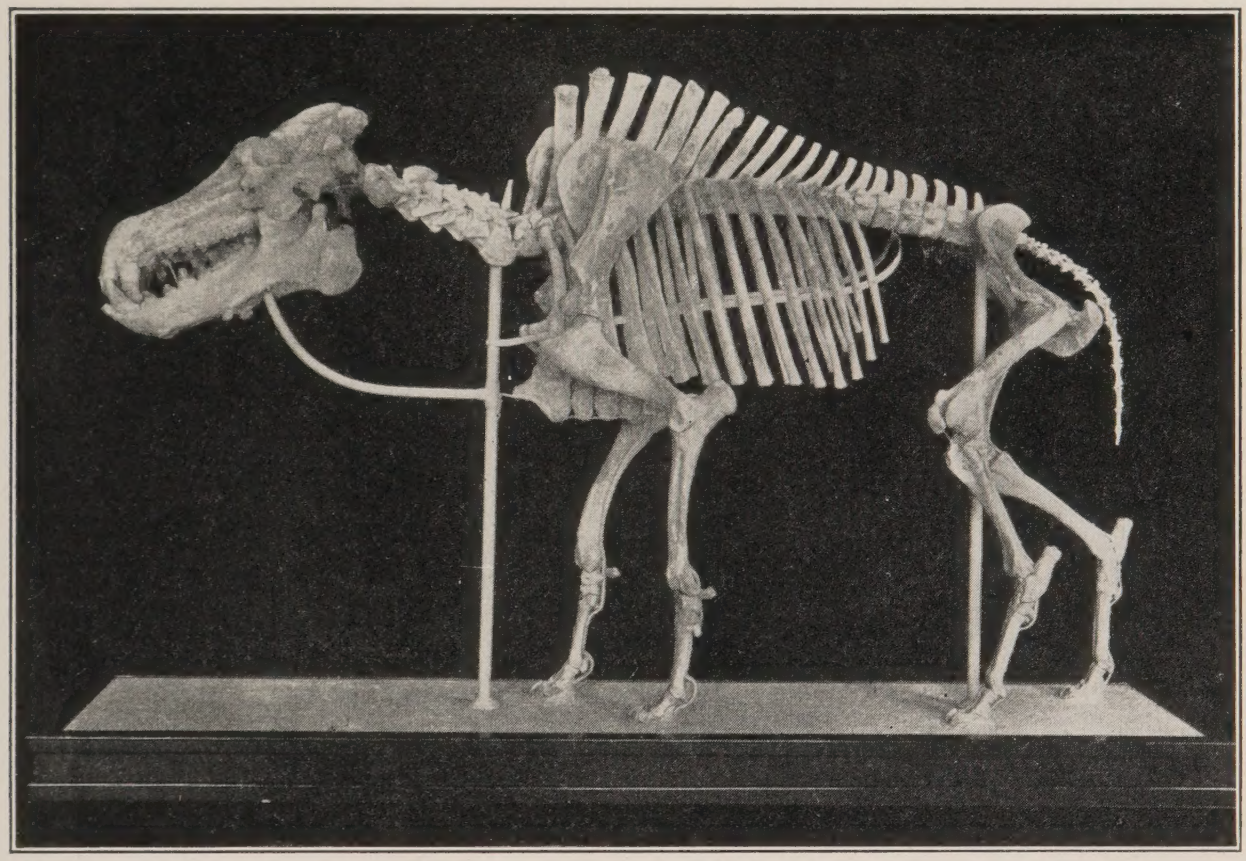


Fig. 80. — Entelodonts of the New and Old Worlds. Skeleton of the giant Upper Oligocene entelodont *Dinohyus hollandi*. In the Carnegie Museum, Pittsburg. After Peterson.

cene characters; they are simply a continuation of the palæotheres, anoplotheres, and last of the xiphodonts of the Upper Eocene or Ludian.

The first real Oligocene fauna is that of the marls of Ronzon (13) in the Rhone valley near Lyons, which succeeds the fauna of the *gypse* or Ludian, and contains the new Oligocene mammals. Of the same age are the mammals of Hempstead (24) (Isle of Wight), of Lobsann (18) (Alsace), Calaf and Tarrega (25, 26) (Spain) numerous deposits in Swabia (19–23), and possibly of Monte Promina in Dalmatia (27).

The mammals of this stage are of three kinds: (1) those descended from the Upper Eocene fauna of Europe; (2) those of fresh north or south Asiatic origin or previously undiscovered; (3) those apparently from

[1] Depéret, L'évolution des Mammifères tertiaires; l'importance des migrations (Oligocène). *C. R. Acad. Sci. Paris*, Vol. CXLII, séa. March 12, 1906, pp. 618 seq.

North America or first known in the Upper Eocene of that region. The conspectus of this fauna is as follows:

Lower Oligocene Group	
a. (*Continued from Eocene*)	
	Palæotheres
	Anthracotheres
	Anoplotheres
	Cænotheres
	Canids (dogs)
	Erinaceids
	Opossums
	Hyænodonts
b. (*New Arrivals*)	
	Rhinoceroses
	Entelodonts
	Gelocids
	Mustelids
	Amphicyonids
	Cricetines (hamsters)

Among the odd-toed ungulates of this assemblage the horses (Equidæ) are conspicuous by their absence. The palæotheres (*Palæotherium, Plagiolophus*) are entering on their decline. The rhinoceroses are represented by a small form (*Ronzotherium*) with subhypsodont molar teeth which appears to be of the river-frequenting, amynodont type rather than a true rhinoceros. Tapirs have not appeared in Europe at this stage.

The last of the anoplotheres occur at this level. Among the even-toed ungulates the entelodonts, supposed migrants from America, are still rare. The anthracotheres are beginning their dominant reign. These animals are purely European in origin, hardy travelers and versatile feeders; they are very widely distributed geographically and form valuable means for time correlation. They are polyphyletic and include hypsodont and brachyodont branches as follows: (1) The typical *Ancodus* (*Hyopotamus*) *velaunus* of Ronzon, with its long-crowned molar teeth, is of the same evolution stage as the animals (*A. bovinus*) found at Hempstead on the Isle of Wight; it is a bit more hypsodont or modern than our *Ancodus* (*A. americanus, A. brachyrhynchus, A. rostratus*) of the great plains of ancient Dakota. (2) The short-crowned anthracothere *Brachyodus* also occurs in the Fayûm of northern Egypt (*B. goringii*), in Dakota (*B. brachyrhynchus*), and at Hempstead. It is descended from the *Catadontherium* of the *Lutetian*. (3) *Anthracotherium* also occurs, an ancestor of the giant Middle Oligocene forms. The anthracotheres[1] also exhibit a divergence into dolichocephalic and brachycephalic forms. There is a wide geographic distribution of the ancodons in Europe, Africa, Asia, and North America. No ancestral forms have been discovered in the American Eocene, and their abundance in the Upper Eocene of Europe and Africa points to migration from the Old World; it would appear that from a north Asiatic center these animals may have migrated independently to Europe, southern Asia, and to North America. The American species occur in four successive levels, and parallel those of Europe in their evolution. Whereas in Europe they disappeared at the close of the Middle Oligocene, in North America they survived to the Lower Miocene, represented by an

[1] Matthew, W. D., Observations upon the Genus *Ancodon*, *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVI, Art. i, Jan. 5, 1909, pp. 1–7.

animal (*Arretotherium*) more or less similar to the last survivor (*Merycopotamus*) in the Miocene of India.

Most interesting among artiodactyls is the newly arriving, small, and primitive ruminant *Gelocus*, which appears in the midst of this varied browsing fauna, a representative of the family Gelocidæ, analogous to the existing chevrotains, and a harbinger rather than ancestor of the varied artiodactyl groups of later periods.

The remainder of the mammal fauna of Ronzon may be partly described in the language of Filhol (1881) as revealing to us an aquatic and riparian

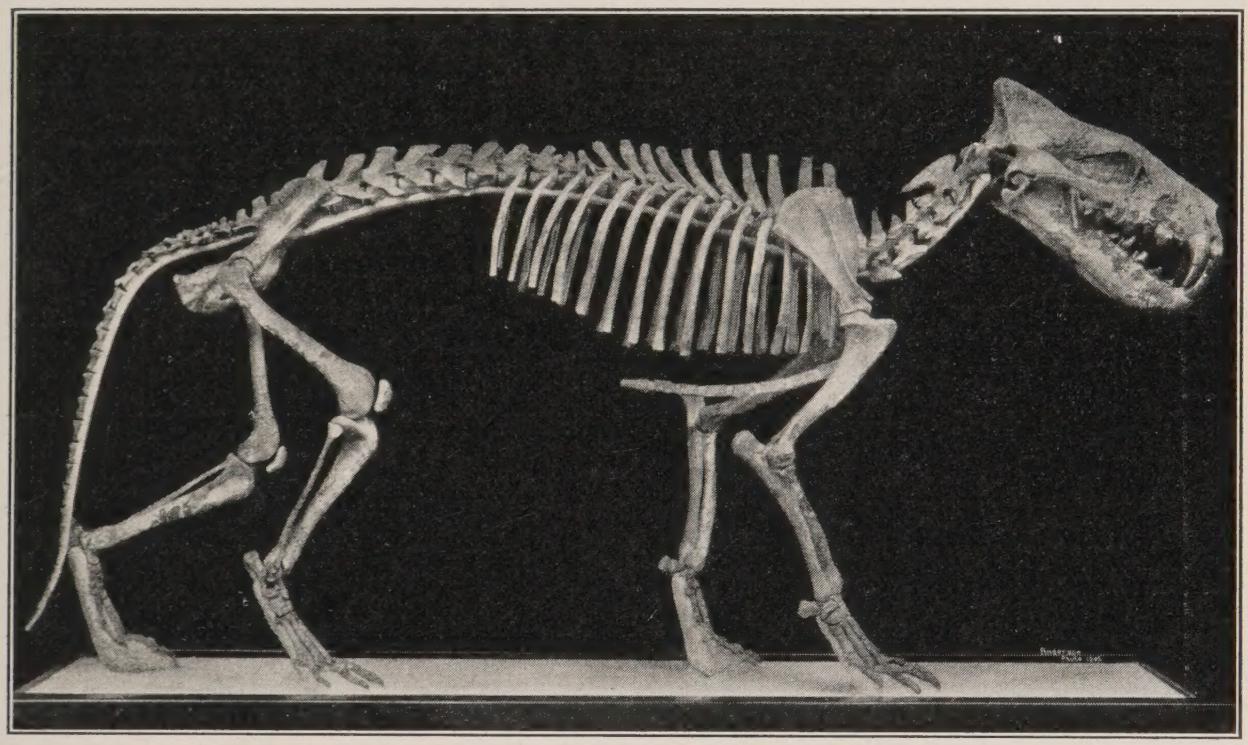


Fig. 81. — Hyænodonts, common to Europe, Africa, and America. Skeleton of the Middle Oligocene creodont *Hyænodon horridus* of South Dakota. In the American Museum of Natural History.

fauna with a few truly terrestrial animals, including also remains of birds, reptiles, fish, insects, crustaceans, and molluscs. The insectivores are represented by primitive hedgehogs, the rodents by chinchilla-like Theridomyidæ, and the hamsters (*Cricetodon*). The opossums (Didelphyidæ) were very small, and for the most part belonged to the *Peratherium* group, which persists with little change from the Upper Eocene. The carnivores are all small forms, excepting the creodont *Hyænodon*. No machærodont cats, or felids, have been discovered at this stage. The canid family is varied, including *Cynodon*, *Cynodictis*, and *Amphicynodon;* the former, in its rather spreading feet, long tail, and shape of the head, suggesting the otter. We wonder at the absence of larger carnivores, for the ungulates are worthy of stronger hunters than those which are known. The Mustelidæ, or marten family, is represented by *Proplesictis;* the otter has not been observed.

Milne Edwards[1] has described the birds of Ronzon as including the Accipitres (*Teracus*), Grallæ, allied to the plovers, also phœnicopterids, including birds allied to the flamingoes but of more slender build and with shorter feet. The gannets are also represented.

Middle Oligocene, Stampian

Upper Tongrian

Our knowledge of the European mammals of this stage extends still more widely, especially to the east of the Adriatic, including a marl deposit as far east as Styria (Austria) (Fig. 82, 48). The rich final deposits of the *phosphorites de Quercy* are of this age. In this age, too, are the lignites of Cadibona (Liguria) (46), the deposits of Moissac (35) in southwestern France, containing the first undoubted paired-horned rhinoceros (*D. minutum*),[2] also of Céreste (22) and Manosque (23) in southeastern France; to the north are the lacustrine sands of Ferté Alais (Seine-et-Oise) (1). In the summit of the Stampian are the lacustrine deposits of Gannat (16) in central France (Allier), which have yielded the large hornless tetradactyl rhinoceros (*A. gannatense*). Altogether Depéret has listed fifty localities, as shown in Fig. 82.

At this time the tree flora was one of sequoias and cinnamons. In northern Italy flourished palms that require an even temperature of 25° C. (77° F.) similar to that of Brazil.

Characteristic mammalian life. — The affinity to America is strengthened by the arrival of fresh perissodactyls, including the first appearance in Europe of the tapirs (*Protapirus*, *Paratapirus*), of the true hornless rhinoceroses (aceratheres), remarkably similar to those of the Middle Beds of the White River group, Dakota, also of undoubted diceratheres, or pair-horned rhinoceroses. The amphibious rhinoceroses, or amynodonts, are represented by *Cadurcotherium* with hypsodont teeth, in a state of evolution closely similar to that of *Metamynodon* of our western plains. An entire lower jaw of *Cadurcotherium*[3] was found at Bournoncle St. Pierre; there is little doubt that this highly specialized amynodont belongs to the age of Moissac in France. These similarities tend to establish a parallel with the Oreodon and Metamynodon Zones (Fig. 101) of the White River group of South Dakota, which are accordingly regarded as of Middle Oligocene age.

The artiodactyl ruminants increase. — Fresh Asiatic elements make their first appearance; *e.g.* the cervuline deer (*Dremotherium*) which, although hornless, is compared with the existing muntjacs (*Cervulus*) of the southern

[1] Milne Edwards, A., Oiseaux Fossiles de la France, 1869–1871, p. 552.

[2] This dicerathere of Moissac is more progressive in its horn development than any of the ancestral diceratheres of the Oreodon Zones.

[3] Boule, M., Le Cadurcotherium. C. R. *Acad. Sci. Paris*, 1896, Vol. CXXII, pp. 1150–1152.

and eastern parts of Asia, animals which are fond of hilly ground covered with forests, and related to the true deer, or Cervinæ. At the same time the gelocids (*Gelocus*) make their last appearance in western Europe. Arrivals from the northerly regions are the beavers, or castorids (*Steneo-*

FIG. 82. — **Middle Oligocene.** Stampian or Upper Tongrian. FRANCE. — Sables de **1** *la Ferté-Alais*, in Paris basin, lacustrine. In the basin of the Allier and the upper Loire: **2** *Bournoncle-Saint-Pierre*, **3** *Bons*, **4** *Perrier, Autrac, Solignat, Orsonnette, Malhat, Les Pradeaux, Les Chauffours, Bansat, Chibrac, Jussat, Romagnat, Pérignat, Lemdes, Cournon*, **5** *Montaigut-le-Blanc*, **6** *Champeix*, **7** *Saint-Germain-Lembron, Boudes*, **8** *Antoingt*, **9** *Vodable*, **10** *Lamontgie*, **11** *Nonette*, **12** *La Sauvetat*, **13** *Gergovia*, **14** *Marcoin*, **15** *Chaptuzat;* lacustrine deposits of **16** *Gannat;* **17** *Saint-Menoux*, **18** *Vaumas*, **19** *Saint-Pourçain-sur-Bèbre*, **20** *Briennon*, **21** *Digoin*. Schistes de **22** *Céreste*, near Aix. Gypse et marnes, lignites de **23** *Manosque*, near Aix (600 meters). Argiles de **24** *Saint-Henri*, near Marseilles. Calcaires gypsifères de **25** *les Milles*, near Aix. **26** *Auzon* (Gard). **27** *Perne* (Vaucluse). In the Garonne basin: **28** *Cestayrol*, **29** *Saint-Sulpice*, **30** *Rabastens, hill of Saint-Martin, l'Isle d'Albi*, **31** *Montans;* mollasse de **32** *Salvagnac*, **33** *Villebramar; Pont-Sainte-Marie, Capellier, Les Péries, la Milloque, Comberatière, Itier, Bourg de Visa*, **34** *Tournon;* mollasse de **35** *Moissac;* **36** *Beauville*, **37** *Montségur;* phosphorites de **38** *Quercy* (greater part). GERMANY. — Meeressande von **39** *Ufhofen*, in central Germany. Septarienthon von **40** *Flonheim*, near Mayence. Cyrenen-Mergel von **41** *Miesbach* (Bavaria). Braunkohlenlagerung von **42** *Schlüchtern*, **42a** *Gusternhain*, **43** *Westerwald*, in southwestern Prussia. SWITZERLAND. — **44** *Blauen*, near Basel. **45** *La Conversion*, near Lausanne. ITALY. — Lignitic deposits of **46** *Cadibona* (Liguria), **47** *Monteviale, Zovencedo* (Vicenza). AUSTRIA. — **48** *Trifail* (Styria). **49** marls in *Dalmatia*. ISLAND OF MAJORCA. — Lignites of **50** *Inca*. Correlation of Depéret.

fiber). Among insectivores appear the water voles, desmans or myogalids, also the shrews or soricids (*Amphisorex*). Among rodents there also appear the lagomorph picas or tailless hares (Lagomyidæ, *Titanomys*), animals which are at present distributed in the mountainous parts of Asia, eastern Europe (one species), and North America (one species).

Among animals of prey, representatives of the true cats (Felidæ, *Pseudælurus*) first appear, and in the streams for the first time the otters (*Potamotherium*) occur. Probably also from northern Eurasia or from America arrived the first of the saber-tooth cats (Felidæ-Machærodontinæ); it is noteworthy that machærodonts (*Dinictis*) are also first known in the Lower Oligocene of our western plains.

Still greater variety is lent to the mammalian fauna by the entrance either from southern Asia or from Africa of representatives of two of the

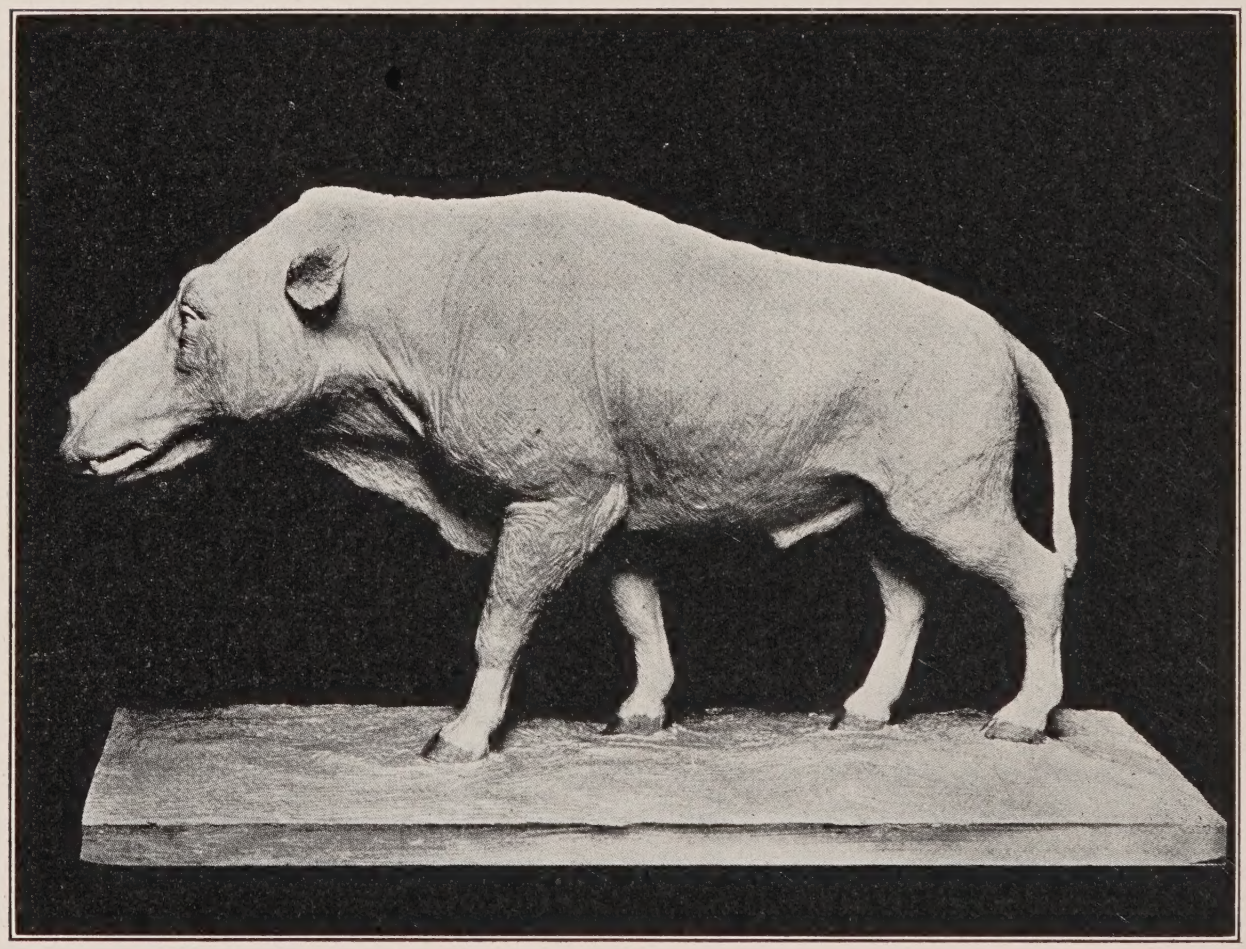


Fig. 83. — Entelodonts of the New and Old Worlds. Model of the giant Upper Oligocene entelodont *Dinohyus hollandi* of western Nebraska. From original by Theodore A. Mills, executed under the direction of O. A. Peterson, in the Carnegie Museum, Pittsburg.

edentate orders, the aardvarks (Tubulidentata), which are represented by the archaic *Archæorycteropus*, and the pangolins, or scaly anteaters, represented by *Leptomanis*. Since these animals have not as yet been found in the Lower Oligocene of Africa, it is uncertain whether they are of African or of Asiatic origin; on the whole, the evidence favors their northerly or Asiatic origin; the pangolins are widely distributed in the later Cænozoic of Asia.

Altogether this assemblage, as listed by Depéret, is a most imposing one. As shown in the accompanying conspectus, mingled with these new migrant or foreign forms we find the continuation of the greater part of the Lower Oligocene mammals as listed on p. 188.

The members of this fauna that are dying out are the hyænodonts, palæotheres, and entelodonts. The apparent extinction of these giant pigs (entelodonts) in Europe is noteworthy, because in America they survive to the summit of the Oligocene or Lower Miocene and attain an enormous size. They also are recorded (*Tetraconodon*) in Miocene or Pliocene deposits of India.

CHARACTERISTIC MAMMALS

Amynodonts
(*Cadurcotherium*)
Palæotheres, last appearance
Chalicotheres
Entelodonts, last appearance
Hyænodonts, last appearance
Anthracotheres of large size
Rodents of many existing families
Insectivores of many existing families
Amphicyonids
Machærodonts
Lutrines, or otters
Viverrids
Pangolins, scaly anteaters
Aardvarks, orycteropids

The Oligocene faunal approximation to America is the closest at this stage. The continued absence of horses is very remarkable; it is doubtless due to the prevalence of forests and the absence of open plains. The anthracotheres attain a large size. The aceratheres, hornless rhinoceroses, are very similar in their dental evolution to those of Dakota. The pair-horned rhinoceroses (*Diceratherium minutum*) are more advanced in the development of their horns than those of the White River Group of Dakota. The chalicotheres are represented by *Schizotherium*, a more advanced stage than the *Pernatherium* of the Upper Eocene of France. On the whole, the fauna is still that of river and lake borders, of forests, streams, and small meadows and glades.

UPPER OLIGOCENE, AQUITANIAN

This is the age typified by the mammals of the famous lacustrine beds of St. Gérand-le-Puy (Allier) (Fig. 84, 2) in the heart of France. Of nearly identical age in America are the Middle and Upper beds of the John Day Formation in Oregon, as indicated by similar stages in the evolution of the mammals. In the Old World, while the localities as listed by Depéret[1] are only eighteen in number, they may be traced as far east as Hungary. In Germany are the rich deposits of Eggingen (11) near Ulm. In Savoy, on the borders of Switzerland, Depéret has unearthed at Pyrimont (4) a fauna which promises to be richer and more complete even than that of St. Gérand-le-Puy.

As noted on p. 183, Europe has now taken on its modern outlines. This is a period of great bodies of freshwater, partly bordered with deciduous trees of modern type. The deposits of St. Gérand-le-Puy, of Pyrimont (Savoy), of Weisenau near Mayence, and of Ulm in the basin of the Upper

[1] Depéret, L'évolution des Mammifères tertiaires; l'importance des migrations (Oligocène). *C. R. Acad. Sci. Paris*, Vol. CXLII, séa. March 12, 1906, p. 618.

Danube mark a long band across western and central Europe over which ranged a very typical and very homogeneous mammalian fauna.

Declining groups. — There are marked extinctions or emigrations. The absentees among the recorded mammals of this Aquitanian stage are the palæotheres, amynodonts or cadurcotheres, the entelodonts or giant pigs, the gelocids (*Gelocus*), as well as their enemies the carnivorous hyænodonts. With these exceptions the Middle Oligocene or Stampian mammals (p. 193) probably all continue at this time. Yet it is certain that we have here

Fig. 84. — **Upper Oligocene.** Aquitanian. FRANCE. — Calcaire de **1** *Celles-sur-Cher*, **2** *Saint-Gérand-le-Puy*, in the Bourbonnais, lacustrine formation. **3** *Chaveroche*, in the Bourbonnais. Conglomérat et sables de **4** *Pyrimont*, marnes de *Challonges*, in Savoy. **5** *Varages*, in Provence. Grès mollassique de **6** *Boujac*, near Alais (70–80 meters). Mollasse d' **7** *Avignon*, in Rhone valley. GERMANY. — Kalke von **8** *Weisenau*, **9** *Mombach*, near Mainz. **10** *Haslach*, in southwestern Germany. Kalk und Mergelbänke von **11** *Eggingen*, near Ulm. SWITZERLAND. — Mollasse grise de **12** *Lausanne*, on Lake Geneva, fresh water with a marine band (300 meters). **13** *Othmarsingen*, near Zürich. Mollasse à lignites de **14** *Hohe Rhonen*, near Basel. SPAIN. — Marls and limestones of **15** *Rubi*, near Barcelona. AUSTRIA-HUNGARY. — **16** *Tuchorschitz* (Bohemia). **17** *Keutchach* (Karinthia). **18** *Waitzen* (Hungary). Correlation of Depéret.

only a partial picture of the Old World life of the times, because the only mammals known are those adapted to lowlands and lake and river borders. Highly distinctive are the giant anthracotheres (*A. magnum*), the last of this large phylum, although the smaller, short-crowned anthracotheres (*Brachyodus*) survive into the Miocene. Among diminutive forms the opossums or didelphids make their last recorded appearance (*Amphiperatherium*) in the Old World.

Mammals and birds. — The mammalian group was picturesquely described by Filhol [1] in 1880 in his memoir on St. Gérand-le-Puy, and other scenes in central France at this Middle Oligocene time may be imagined from Milne Edwards' description [2] of the birds of St. Gérand-le-Puy and other localities in the Allier basin. The lakes were small and shallow, surrounded by broad belts of marsh with characteristic vegetation. Turtles of various kinds lived in the waters, and crocodiles almost as large as the living Nile types were a constant menace to the aquatic birds. The varied bird population finds its parallel to-day on certain lakes in the interior of Africa. Unlike the avifauna of the Upper Eocene, it begins to include a number of existing genera. The pelican, ibis, marabou, flamingo, sandgrouse, and above all the courroucou (trogon), the parrots, and secretary birds lent to this fauna an unmistakable African aspect. Ducks were common, cormorants (*Graculus*) and grebes (*Colymboides*) were less abundant than the gulls (*Larus*), which are to be seen everywhere. Considering this abundant community of bird life with that of modern Africa, it is very noteworthy that no African mammals whatever have been found in any deposits of this period. The birds are forms which could more readily migrate. Probably the modern African avifauna is largely derived from that of Oligocene Europe and Asia.

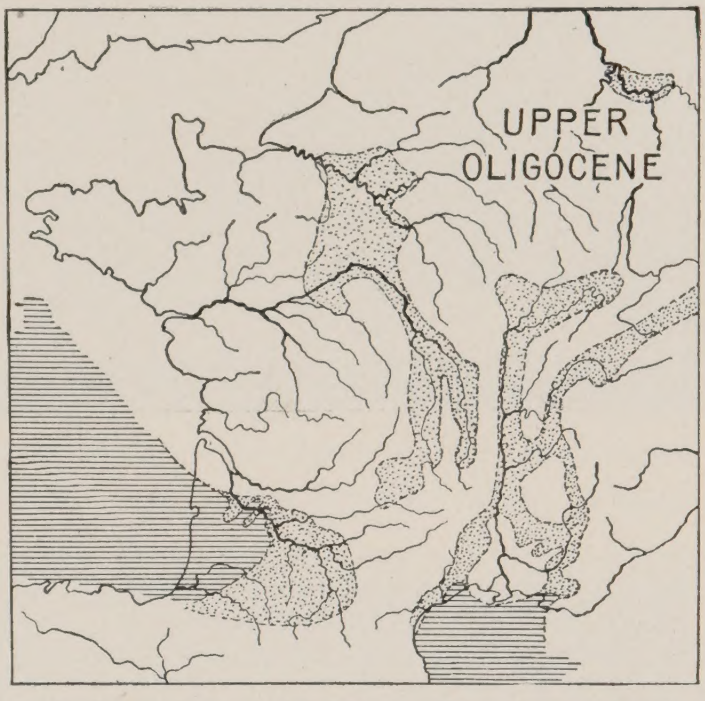


FIG. 85. — France in Upper Oligocene or Aquitanian times. Dotted areas = lagoons. White = land. Ruled = sea. After de Lapparent, 1906.

As noted above, the mammal fauna preserved probably presents a very incomplete picture of the manifold animal life of France at this time. Thus it seems likely that monkeys and lemurs inhabited the forests, and that bats were much more numerous than the one genus found would indicate. Horses may have existed on the northeastern plains; but no proofs have been found that they existed in Europe. Rodents were common, represented by six families, namely, the now extinct theridomyids (*Theridomys*) and eomyids (*Rhodanomys*), also the squirrels (*Sciurus*), beavers (*Steneofiber*), the tailless hares or picas (*Titanomys*). We especially note the

[1] Filhol, H., Étude des Mammifères fossiles de Saint-Gérand le Puy (Allier). *Bibl. École Hautes Études, Sect. Sci. Nat.*, Vol. XIX, Art. 1., 1880.

[2] Milne Edwards, A., Oiseaux fossiles de la France, 1869–1871, pp. 562–570.

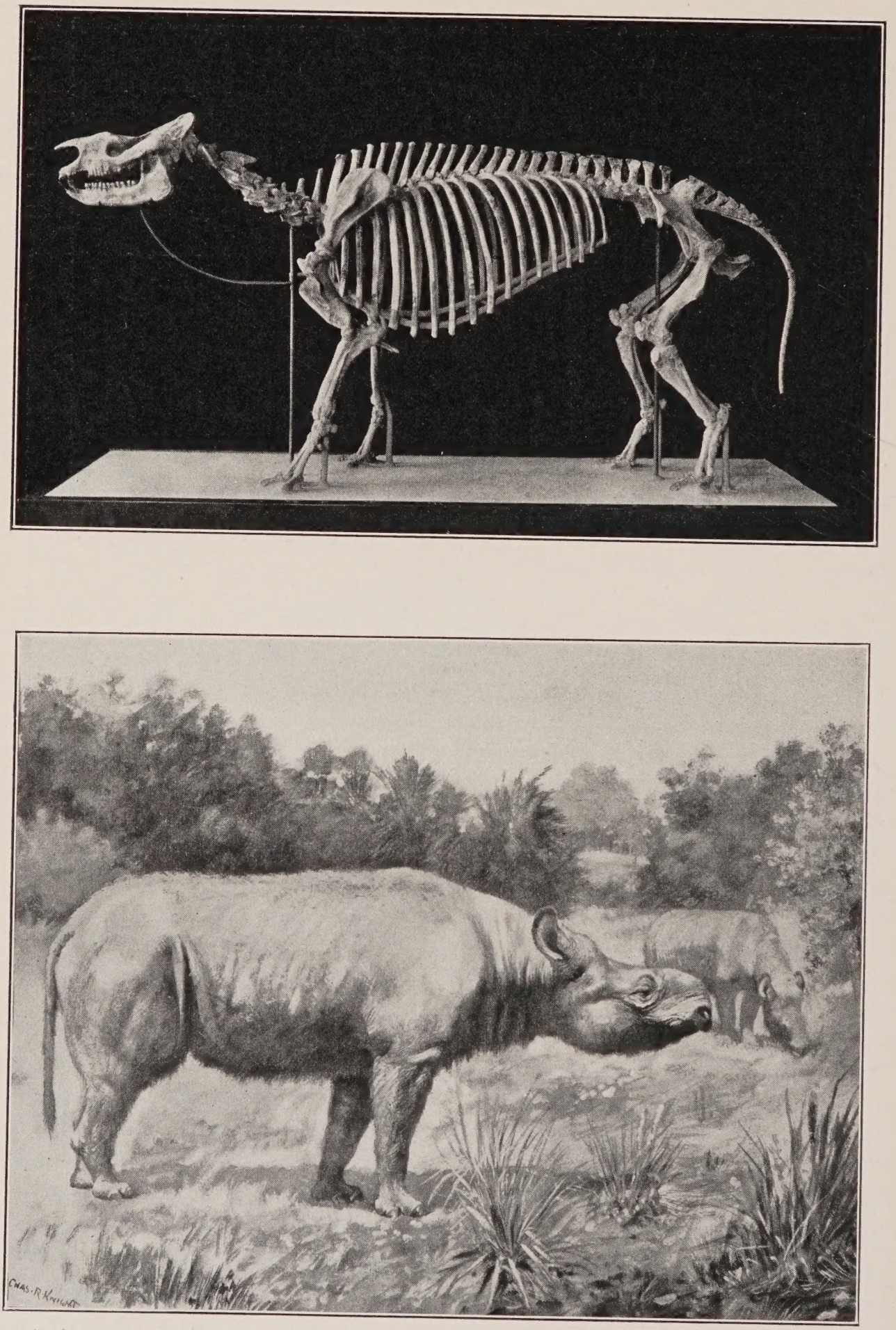


Fig. 86. — Diceratheres, common to the New and Old Worlds. Above: Skeleton of the Oligocene rhinoceros *Cœnopus occidentalis* of South Dakota. Below: Restoration of the same by Charles R. Knight. Both in the American Museum of Natural History.

absence of the true rabbits and hares (Leporidæ), which at this time were abundant in America.

PREVAILING MAMMALS

Suillines
Cænotheres
Cervuline Deer (hornless)
Giant Anthracotheres
Aceratheres
Diceratheres
Tapirs
Chalicotheres
Opossums
Amphicyonids
Civets
Castorids (*Steneofiber*)

The carnivores have undergone great changes since the Lower Oligocene. The civet-like dog *Cynodictis* has disappeared. The canids are now represented by two more modern genera (*Amphicynodon*, *Cephalogale*). The largest dog-like forms are the amphicyons, now equaling the wolf or hunting dog in size, but not in speed; the typical members of this race were heavier and more thickset than the dogs, but more slender than the bears, with clumsy legs and a long tail. Of the smaller Carnivora, the mustelid family is represented by *Plesictis*, a small, long-bodied carnivore of the size of a marten, as well as by the otters. The mustelines are also represented by *Proœlurus*. Still more striking is the presence of the fierce viverrid carnivores (*Amphictis*, *Herpestes*) of the modern civet and mongoose types. Ungulates were numerous, including the tapirs as well as rhinoceroses and chalicotheres. The horses are still absent. The rhinoceroses now embrace the diceratheres and the larger aceratheres (*A. lemanense*). The chalicotheres have now attained a larger size (*Macrotherium*). Also frequenting the vast swamps surrounding the lake were the hornless cervuline deer (*Dremotherium* and *Amphitragulus*); it is noteworthy that this is the last record of this hornless race in Europe. The little cænotheres, the last survivors of the anoplothere family, lived in large herds around the lake, and are found in great abundance. The suillines are represented by the aberrant pigs (*Palæochœrus*).

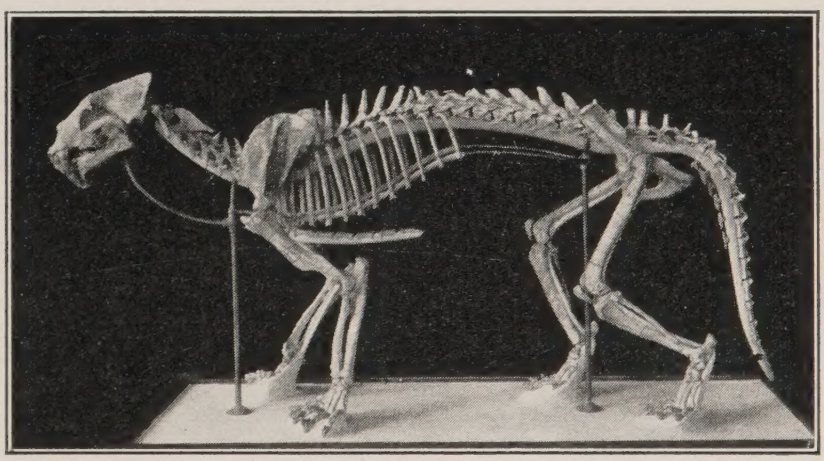


FIG. 87. — Ancestral saber-tooth tigers common to the New and Old Worlds. Skeleton of the Middle Oligocene carnivore *Hoplophoneus primœvus* of South Dakota, a forerunner of the great saber-tooth tiger of the Pleistocene. In the American Museum of Natural History.

At Pyrimont[1] we obtain an imperfect picture of the animal life of the swampy Rhone valley of Savoy toward the close of the Oligocene period.

[1] Depéret and Douxami, Les Vertébrés Oligocènes de Pyrimont-Challonges (Savoie). *Mém. Soc. Paléont. Suisse*, Geneva, Vol. XXIX, 1902, pp. 84–87.

The insectivores are represented by large numbers of a small aquatic animal (*Echinogale*) allied to the desmans. The beavers are also abundant here (*Steneofiber eseri*), animals about one-third smaller than the existing beavers. The Herbivora are the preponderating element of the fauna. Both the two-horned (*Diceratherium*) and the small hornless (*Aceratherium*) rhinoceroses occur. The tapirs (*Paratapirus*) were somewhat larger animals than the Middle Oligocene *Protapirus*. Of the suoids *Palæochœrus* is the precursor of the Miocene *Hyotherium;* the very primitive, long-headed pig *Doliochœrus* also occurs. The small and graceful mem-

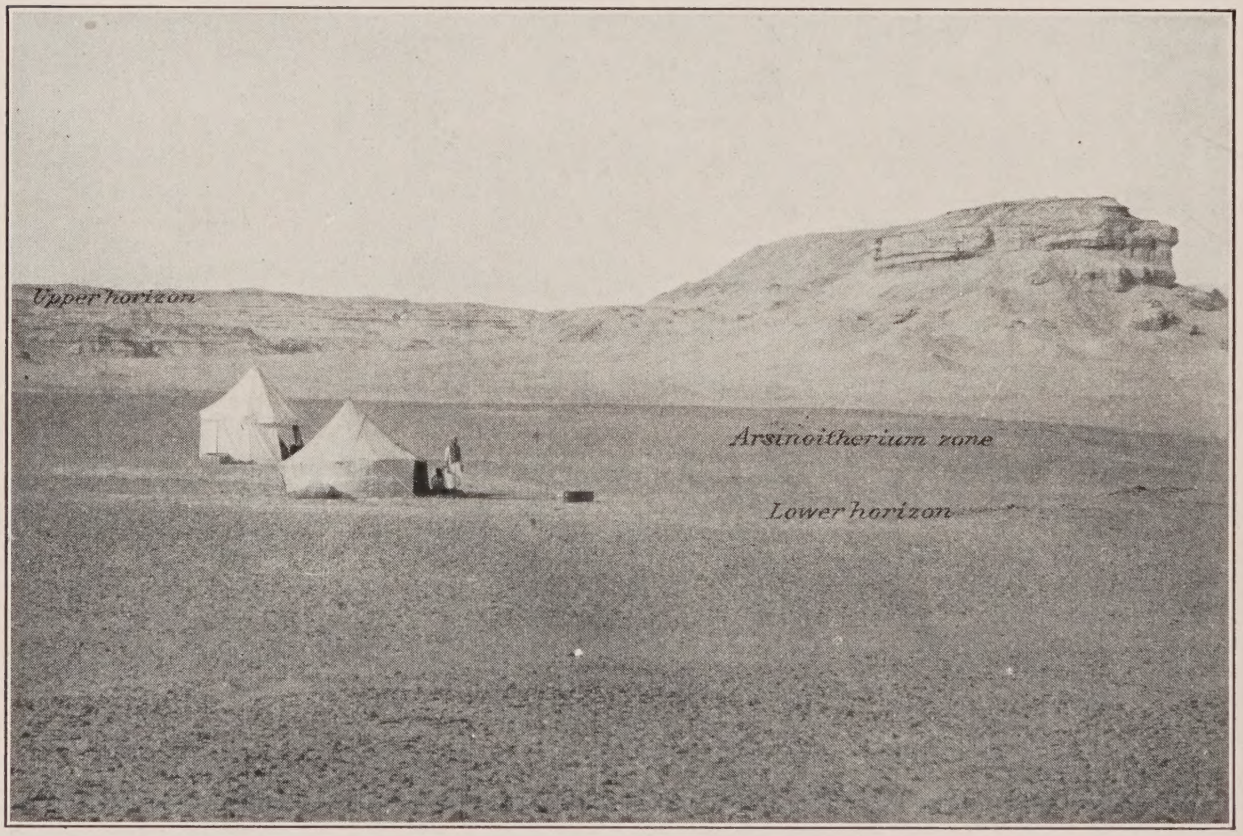


FIG. 88. — Lower Oligocene fluvio-marine formation, north of Lake Qûrun, Fayûm, Egypt. Lower and upper horizons of the Arsinoïtherium zone. Photograph by American Museum of Natural History, expedition of 1907.

bers of the genus *Cœnotherium* lived in large troops in the region of Pyrimont.

Oligocene suillines. — Stehlin inclines to the belief [1] that both kinds of true pigs (*Propalæochœrus, Doliochœrus*) which appear at the beginning of Oligocene times in Europe are new immigrants and not descendants of *Chœromorus* or of any other Eocene suillines of Europe (see p. 148). Of these Oligocene pigs *Propalæochœrus* is regarded as the starting point of the Old World main group of true pigs with all its branches, while *Doliochœrus* exhibits such striking resemblances to the peccaries (Dicotylidæ) of North America that Stehlin considers it very near the stem form if not the actual stem form of our Oligocene group of primitive peccaries. The

[1] Stehlin, H. G., Die Säugetiere des schweizerischen Eocæns, 1903–1906, p. 749.

Old World Miocene pigs (*Listriodon*, *Chœrotherium*, see p. 253) are at best regarded as aberrant branches of the main Old World (*i.e. Propalæochœrus*) stem.

II. UPPER EOCENE AND OLIGOCENE LIFE OF AFRICA

The epoch-making discoveries of recent years in Egypt have already been briefly referred to (p. 72), and now deserve a fuller treatment. On

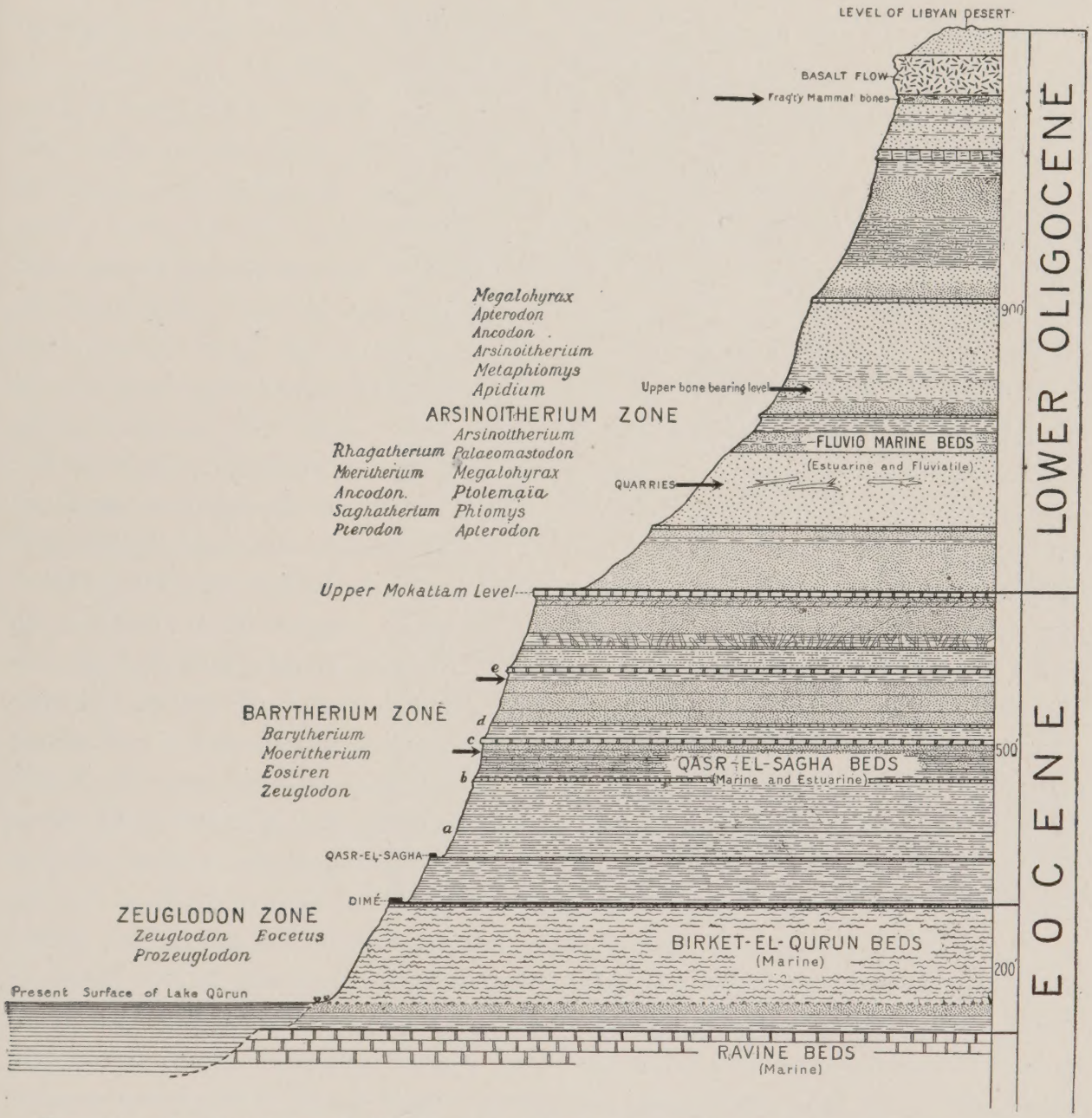


FIG. 89.—Section through the Eocene and Oligocene formations north of Lake Qûrun, Fayûm, Egypt. Arrows indicate levels richest in remains of mammals. After Beadnell, Andrews, Granger, Osborn.

the southern borders of the Libyan Desert, sixty miles southwest of Cairo, lies a series of bluffs of Upper Eocene and Oligocene age, overlying the fertile basin of the Fayûm. As early as 1879, Schweinfurth discovered some bones of the great Eocene whales among the lower westerly bluffs of what may be known as the Zeuglodon Zone (Fig. 89). In 1898 came the

first evidence of the existence of extinct land animals in this region, and in 1901–1905 explorations under Beadnell and Andrews of the Egyptian Survey and British Museum resulted in a series of remarkable discoveries, which were ably set forth in Andrews' fine memoir of 1906.[1]

Supplementary explorations by the author, and Mr. Granger of the American Museum,[2] in 1907, and by other institutions, promise to round out our knowledge of this newly found world of African life in early Tertiary times.

As shown in the accompanying section, the bluffs are sixteen hundred feet in thickness. The lower level, or 'Zeuglodon Zone' (200 feet) is a purely marine formation rich in remains of the primitive Eocene Cetacea (*Zeuglodon* and *Prozeuglodon*). Above these (500 feet) are marine and estuarine beds in which remains of *Zeuglodon* are mingled with those of fluviatile and shore-living mammals, including sea-cows (*Eosiren*), amphibious animals (*Mœritherium*) related to the proboscidean stock, and still larger quadrupeds (*Barytherium*) of unknown affinity; this may be termed the 'Barytherium Zone' and is believed to be of Upper Eocene age from evidence afforded partly by the animals, partly by richly fossiliferous shell layers. Above this are fluvio-marine beds (900 feet), designated as the 'Arsinoïtherium Zone,' which yield a splendid representation of the land fauna of northern Africa in Lower Oligocene times. Beside the mammals we here discover giant land tortoises (*Testudo ammon*) resembling those of modern Madagascar, giant pythons (*Gigantophis*), ostrich-like birds (*Eremopezus*), broad-snouted crocodiles (*Crocodilus megarhinus*) similar to those now found in African rivers, as well as the slender-snouted gavial-like forms (*Tomistoma*) similar to those now found in Borneo. In the rivers beside the numerous sirenians and zeuglodont-whales there swam river turtles (*Podocnemis*) related to those found to-day only in South America; there were also large sea snakes (*Pterosphenus*), and in the Mediterranean Sea near by were found great floating leather-back turtles (*Thalassochelys*) closely similar to modern forms.

So far as the mammals mirror their surroundings, Eocene Libya was a savannah country, partly open, partly thicketed or jungled, partly forested, of about the same temperature as to-day, fairly well watered, and subject to occasional freshets and floodings from sand-bearing rivers to the south. These old river beds of loosely compacted sand have yielded the greater part of the thousands of isolated specimens which have been taken from this region, including forty-five species of mammals, twenty-one of reptiles, and twenty-three species of fishes.

The fauna as a whole shows affinities to that of the modern life of

[1] Andrews, C. W., A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. 4to, London, 1906.

[2] Osborn, H. F., Hunting the Ancestral Elephant in the Fayûm Desert. *Century Magazine*, Vol. LXXIV, no. 6, October, 1907, pp. 815–835.

Africa, Asia, and South America, also to the life of Eocene-Oligocene Europe. This assemblage, however, presents more contrasts than resemblances to the mammalian life which existed in Lower Oligocene times on the north shores of the Mediterranean, as displayed in the phosphorites of Quercy.

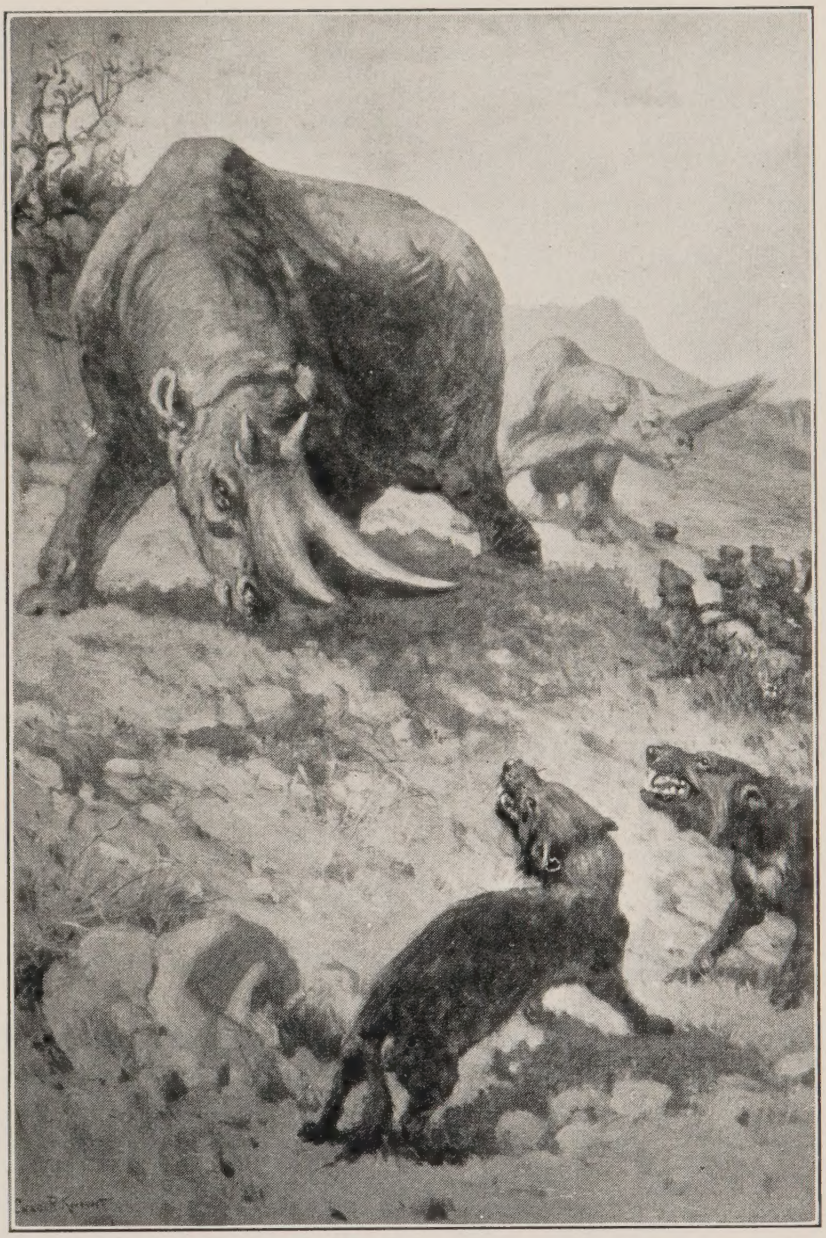


Fig. 90. — The aberrant rhinoceros-like ungulate *Arsinoïtherium* attacked by the carnivorous creodont *Pterodon*. (Oligocene of the Fayûm, Egypt.) After original by Charles R. Knight in the American Museum of Natural History.

The *resemblances* consist in the presence of small myomorph rodents (*Phiomys*, *Metaphiomys*),[1] and a great variety of carnivorous creodonts belonging exclusively to the family Hyænodontidæ, including the three principal genera *Hyænodon*, *Pterodon*, *Apterodon*, also found in France. Among the even-toed ungulates, or artiodactyls, we find in northern Africa, as in Europe, several ancodonts or hyopotamids (*Ancodus*, *Brachyodus*); the aberrant *Rhagatherium* of North Africa is also found in Switzerland; there are large mammals (*Geniohyus*) resembling the European suillines in their dentition, and very diminutive forms (*Apidium*) resembling remotely *Acotherulum* and *Cebochœrus* of France.

The very striking point of *contrast* with the neighboring peninsula of Europe is the *absence* of perissodactyls, of tapirs, horses, and rhinoceroses of all kinds. Neither are there any higher types of selenodont artiodactyls such as we might consider as ancestral forms of the great ruminant fauna of modern Africa. This would appear to strengthen the

[1] Osborn, H. F., New Fossil Mammals from the Fayûm Oligocene, Egypt. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, Art. xvi, Mar. 25, 1908, pp. 265–272.

hypothesis that both the Perissodactyla and Artiodactyla are natives of Holarctica, or the northern hemisphere.

CHARACTERISTIC MAMMALS

Creodont-carnivores
  5 genera
Ptolemaïds
  Relationships unknown
Myomorph rodents
Anthrocotheroid artiodactyls
  2 genera
Suoid artiodactyls
  2 genera
Hyracoids, or hyraces
Primitive proboscideans
  sub-aquatic and terrestrial
Barytheres
Arsinoïtheres
Sirenians
Zeuglodonts

The great arsinoïtheres played the part in Oligocene Africa which is now performed by the rhinoceroses in the dark continent: they were the giant mammals of the period. The dominant feature of the head is a pair of enormous forwardly-projecting bony horn-cores over the snout, which in life were sheathed with horn, sharply pointed in the old bulls, and blunted or rounded in the calves. A smaller pair of horns are also seen to rise above the eyes. As restored by Andrews, a moderate-sized bull (*Arsinoïtherium zitteli*) stands five feet nine inches at the withers. The neck is short, the limbs long, the feet short and spreading, terminating in five short toes adapted, like the crested grinders, to grazing. These remarkable mammals, the affinities of which are entirely unknown, were apparently confined to Africa.

Remains of hyracoids are very numerous, indicating that they ran in herds composed either of large varieties (*Megalohyrax*) equaling the smaller

By permission of the Century Company.

FIG. 91. — The extinct giant coney *Megalohyrax* of the Lower Oligocene of North Africa, together with its small successor, *Hyrax*, of recent times. After a drawing by Charles R. Knight.

tapirs in size, or of the smaller but still more abundant *Saghatherium*. All these animals have an enlarged pair of fighting tusks, and the dentition throughout is remarkably similar to that of the existing hyraces, or

coneys of the Sinaitic Peninsula and of Africa. The living hyraces are relatively of diminutive size. It would appear from the varied nature and abundance of these animals that Africa was the chief center of their adaptive radiation.

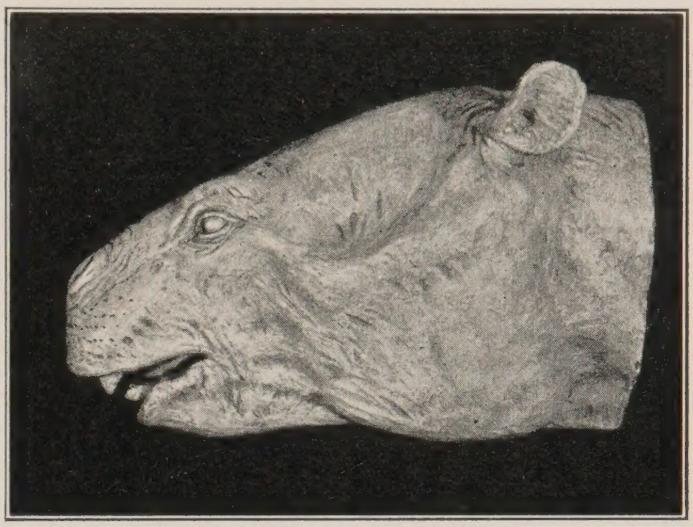


FIG. 92. — Restoration of the head of the primitive proboscidean *Mœritherium* of the Upper Eocene of the Fayûm, Egypt. (The eyes are relatively too conspicuous.) After original, modeled under the author's direction, by Erwin S. Christman in the American Museum of Natural History.

Still more important are the two primitive members of the order Proboscidea, *Mœritherium* and *Palæomastodon*. The former is a sub-aquatic mammal which presents its chief resemblances to the Proboscidea in the enlargement of the same pair of front teeth as those which constitute the tusks of elephants; also in the structure of the grinding teeth, which are essentially ancestral to those of *Palæomastodon*. Other parts of the animal exhibit analogies to the primitive sea-cows or sirenians.

The other type, *Palæomastodon*, appears to be directly ancestral to the Lower Miocene mastodons of Europe; in contrast with *Mœritherium*, it probably possessed a long prehensile upper lip, a pair of spoon-shaped lower incisor teeth which opposed this lip, a pair of upper incisor tusks well developed as fighting weapons, with an enamel band on the outer sides. The grinding teeth are more complex than those of *Mœritherium* and directly ancestral in form to those of *Trilophodon angustidens* of the Lower Miocene of Europe. The accompanying models of the heads (Figs. 92, 93) exhibit the profound differ-

FIG. 93. — Restoration of the head of the primitive proboscidean *Palæomastodon* of the Lower Oligocene of the Fayûm, Egypt. After original, modeled under the author's direction, by Erwin S. Christman in the American Museum of Natural History.

ences between these two proboscideans, and indicate that we may look for other radiations of the proboscidean stock in Africa; possibly the river-living sirenians may prove to be one of these radiations. Certain of the palæomastodons attained an imposing size, but none of them rivaled the arsinoïtheres.

III. OLIGOCENE LIFE OF AMERICA

Geologic conditions. — Widely contrasting with the limited and scattered deposits of Europe are the vast Badlands, or *Mauvaises Terres*, of the

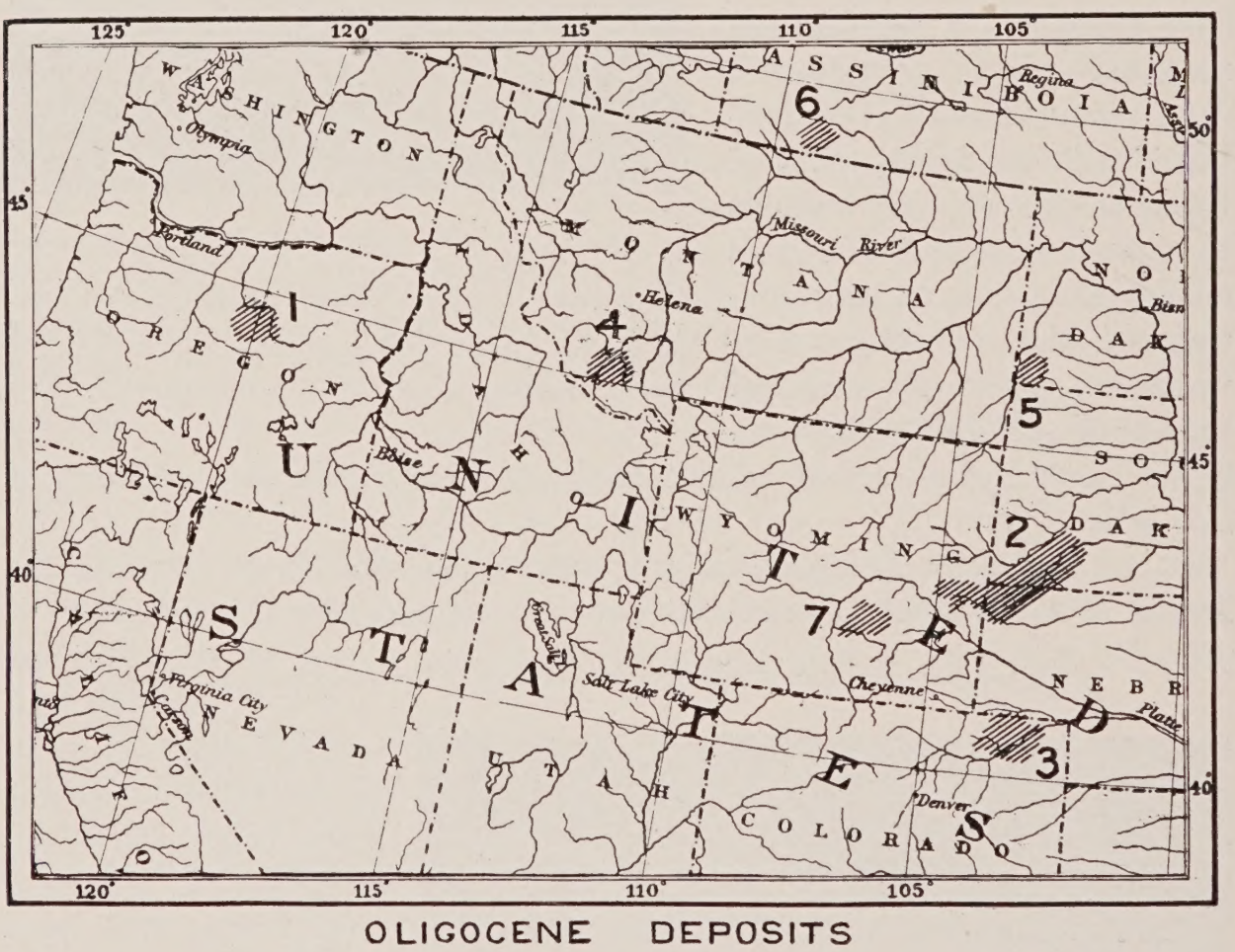


FIG. 94. — Chief Oligocene deposits of fossil mammals in the Mountain Region of North America. **1.** John Day, Oreg. **2.** White River, S. Dak., Neb., Wyo. **3.** Horsetail Creek and Cedar Creek, Col. **4.** Pipestone Creek and Threeforks, Mont. **5.** White Buttes, N. Dak. **6.** Swift Current Creek, Assiniboia. **7.** Bate's Hole, Wyo.

western plains region which, as we now believe, represent the vestiges of extensive flood plains similar to those of many existing rivers in India and South America. Scattered over the surface at different points from British Columbia on the north to the Mexican plateau on the south are areas from two to three hundred miles east of the Rocky Mountains. For the most part they overlie not the Eocene, but the worn upper surfaces of the Cretaceous (Fort Pierre), proving that while the Rocky Mountain basin deposits were forming, the region of the Great Plains was an open, slightly undulating country, traversed by rivers and streams.

The earlier theory as to the origin of these vast deposits was that they were due to great lakes whose borders were frequented by rich mammalian life. As early as 1869 Leidy [1] raised a doubt as to this lacustrine theory in the following words: "While the geological formation makes it appear that the fossils were deposited in ancient lakes, or in estuaries or streams connected with the latter, it is strange that they exhibit no traces of fishes or of aquatic molluscs intermingled with the multitude of relics of terrestrial animals. The single mollusc known is terrestrial, and the turtles are mostly land forms. Even mammals of decided aquatic habitat are absent. With the exception of the shore-living rhinoceros and the beaver, no amphibious mammals have been discovered. While the fossil bones are in perfect preservation, their original sharpness of outline without the slightest trace of erosion indicates quiet water with a soft muddy bottom. . . . The few turtles appear to be related to the swamp-living emydians. It is remarkable that there are no crocodile remains.[2] Where were these creatures when the shores of the ancient waters of Nebraska and Dakota teemed with such an abundant profusion of ruminating hogs and oreodons?"

Despite this sagacious suggestion by Leidy that the mode of preservation of the animal remains did not support the lake theory, this theory was generally maintained by all geologists and palæontologists up to a comparatively recent time. Finally a number of geologists, Gilbert [3] (1896), Haworth [4] (1897), Davis [5] (1900), Johnson [6] (1902) began to throw more and more serious doubts on this theory. Thus Davis observed (1900, p. 372): "Geologists have been too ready to explain the freshwater Tertiary formations of the Rocky Mountain region as lacustrine in origin. The large share of these deposits are probably due to fluviatile or other sub-aerial agencies." The same author drew comparisons with the piedmont, or flood plains of the Ganges, the Po, and the Hwangho. The *coup de grâce* to the lake theory was, however, given by the palæontologists, Matthew [7] (1899, 1901), Fraas [8] (1901) and Hatcher [9] (1902), who set forth convincing reasons for the theory of fluviatile or river channel and flood

[1] Leidy, J., The Extinct Mammalian Fauna of Dakota and Nebraska, Philadelphia, 1869.

[2] Crocodile remains have since been discovered; *see* p. 185, Loomis, 1904.

[3] Gilbert, G. K., The Underground Waters of the Arkansas Valley in Eastern Colorado. *U.S. Geol. Surv.*, 17th Ann. Rept., Pt. 2, 1896, p. 576.

[4] Haworth, E., Physical Properties of the Tertiary (of Kansas). *Univ. Geol. Surv. Kansas*, Vol. II, 1896, p. 281.

[5] Davis, W. M., The Freshwater Tertiary Formations of the Rocky Mountain Region. *Proc. Amer. Acad. Arts Sci.*, Vol. XXXV, no. 17, March, 1900, p. 372.

[6] Johnson, W. D., The High Plains and their Utilization. *U.S. Geol. Surv.*, 22d Ann. Rept., Pt. 4, 1902, p. 638.

[7] Matthew, Is the White River Tertiary an Eolian Formation? *Amer. Natural.*, Vol. XXXIII, 1899, pp. 403–408; and, Fossil Mammals of the Tertiary of Northeastern Colorado. *Amer. Mus. Nat. Hist.*, Mem. 1, Pt. 7, Nov., 1901.

[8] Fraas (ed. by Osborn) on the aqueous *vs.* eolian deposition of the White River Oligocene of South Dakota. *Science*, n.s., Vol. XIV, 1901, pp. 210–212.

[9] Hatcher, J. B., Origin of the Oligocene and Miocene Deposits of the Great Plains. *Proc. Amer. Philos. Soc.*, Vol. XLI, 1902, pp. 113–131.

plain origin, with periods of backwater, lagoon, and shallow lake conditions, and even of æolian conditions. Matthew and Hatcher pointed out that the great Badlands are composed partly of coarse sandstones and conglomerates, indicating river formations, and partly of so-called clays, indicating still water or æolian conditions in which horizontal banded deposits were laid down. Especially interesting is the demonstration by Matthew that the river channel sandstones contain chiefly the remains of forest- and

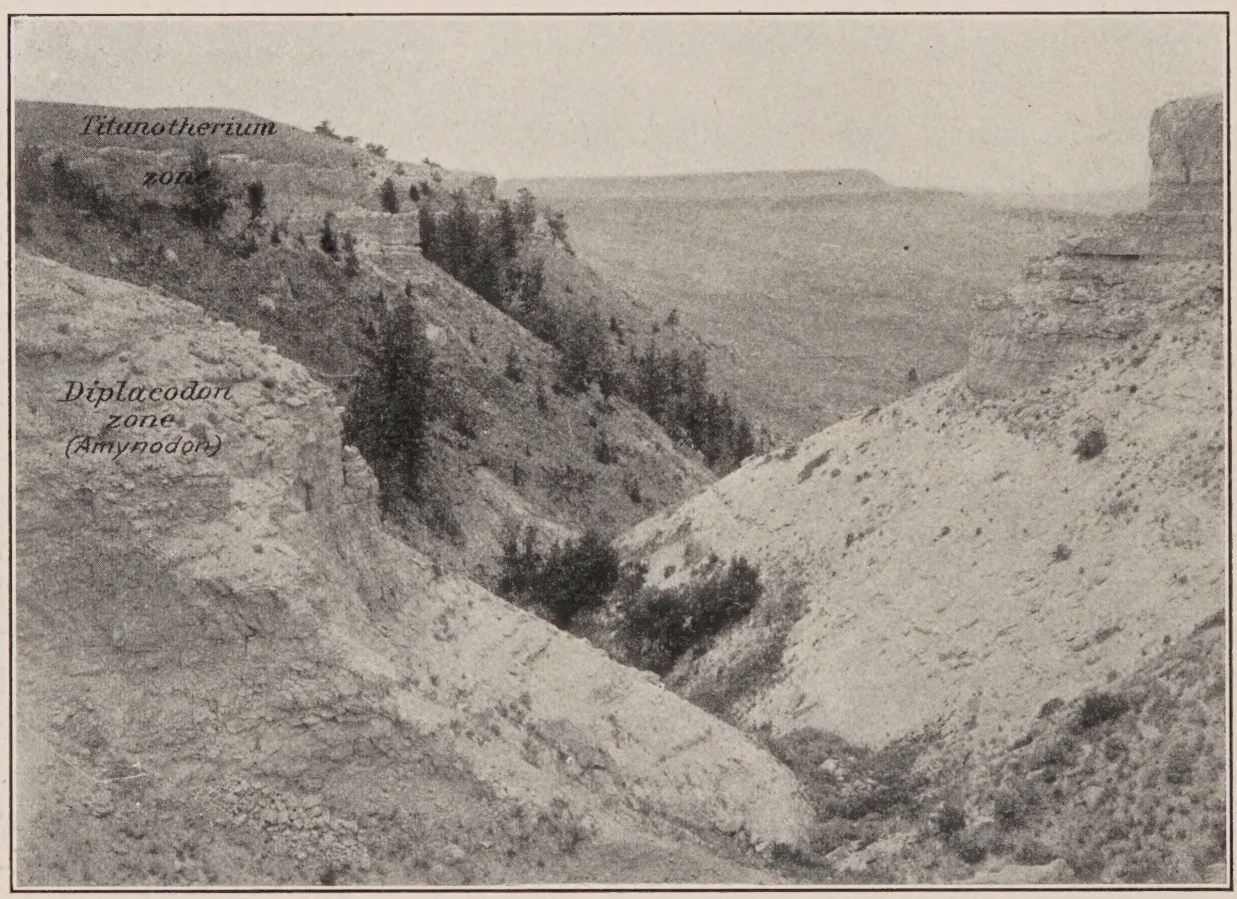
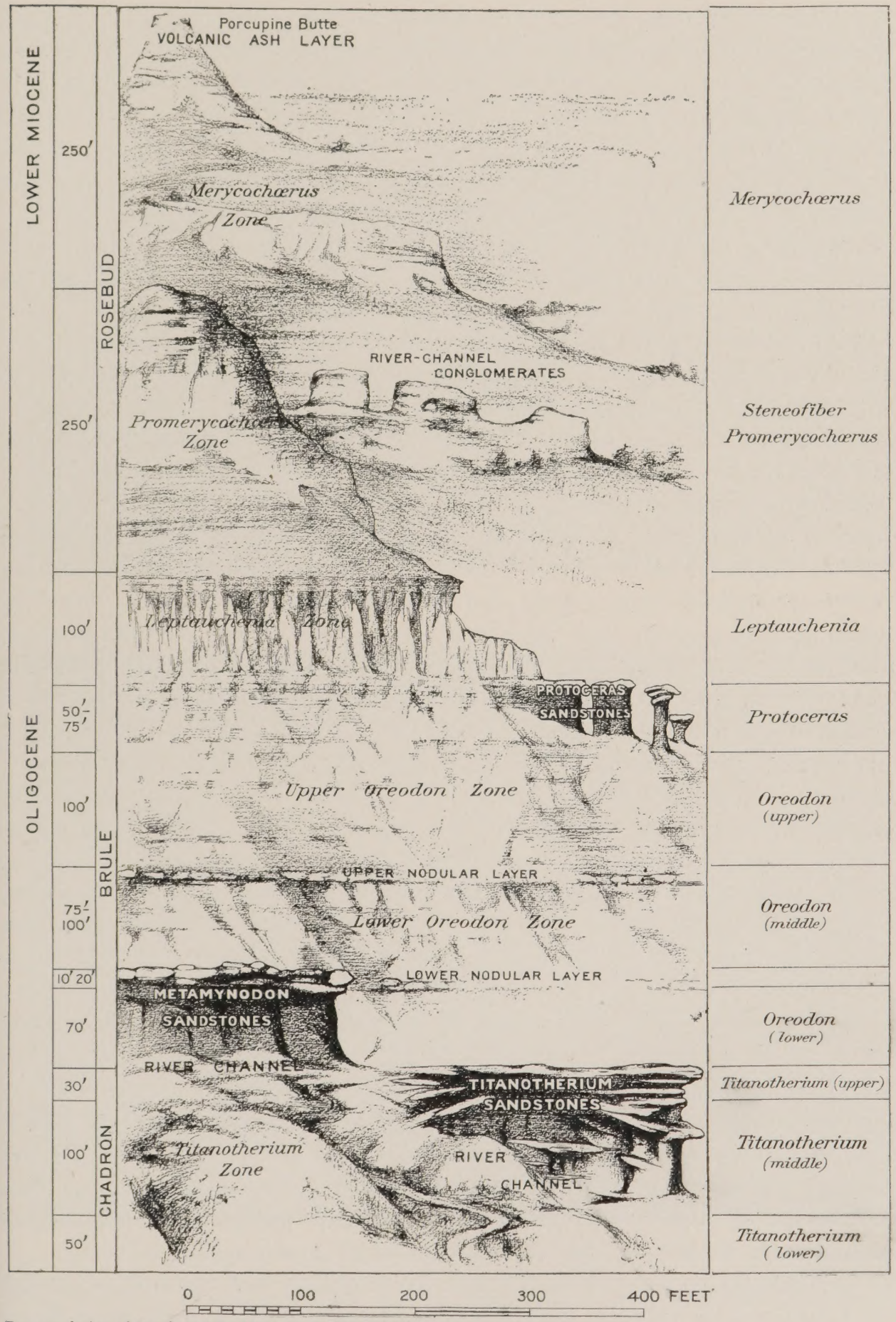


FIG. 95. — Lower Oligocene overlying Upper Eocene horizons on the Beaver Divide at Wagon-bed Spring, near Hailey, Wyo. Diplacodon Zone (Eocene) below; Titanotherium Zone (Oligocene) above. Photograph by American Museum of Natural History, expedition of 1909.

river-living animals, while the fine clays contain the remains of plains-living or cursorial animals.

The accompanying panorama prepared by Osborn after a personal survey of this wonderful region in 1907 is designed to indicate how the fluviatile 'Titanotherium,' 'Metamynodon,' and 'Protoceras' sandstones traverse the outlying fine deposits or clays and prove the existence of great river channels from seven hundred feet to a mile in width. These rivers flowed eastward, and bore down from the mountains coarse materials; they occasionally overflowed in broad shallow sheets of water, too transitory to support any of the aquatic animals. They caused such depositions as are left by the annual overflows of the Nile.

A picture of the plains region in Oligocene times is that of broad, gentle eastward slopes from the Rocky Mountains, plane or gently undulating



By permission of the American Museum of Natural History.

FIG. 96. — Panoramic view of the Oligocene and Miocene exposures on the south side of the White River, South Dakota. After Osborn.

and not mountainous, bearing broad streams with varying channels, sometimes spreading into shallow lakes, but never into vast freshwater sheets. Savannahs were interspersed with grass-covered pampas traversed by broad, meandering rivers. This land was dry in dry seasons, but was flooded in very high water periods. The materials were partly erosion products of the Rocky Mountains and Black Hills, such as true sandstones and conglomerates, but they included also fine layers of volcanic dust, wind-borne from distant craters in the mountains, far out on the plains of Nebraska and Kansas.

Scattered through these Titanotherium and Oreodon beds[1] are numerous thin layers of limestone, always of limited areal extent, rich in remains of freshwater plants (*Chara*) and molluscs (*Limnæa, Physa, Planorbis*), of species inhabiting swamps and small ponds. Remains of forests are found at different horizons throughout these beds, including silicified trunks of trees and seeds belonging especially to forest types (*Hickoria, Celtis*). Nothing like complete trunks are observed, and the impression was that of burial on stream margins where only the less destructible parts of trees would endure sufficiently long to be covered up and preserved. (Hatcher.)

Prevailing mammal types. — It will be observed that in the above described Oligocene mammals of western and central Europe, there are no plains- or upland-living types; horses are absent, the hornless deer-like forms are the gelocids and cervulines, analogous to those now frequenting swampy or forested regions. The dry ground or upland fauna, if it existed, has not been discovered.

In America, on the other hand (see p. 220), both the low ground and the high ground mammals of the Oligocene are known, the former broadly agreeing in foot and tooth structure with those of Europe; the latter, including the horses and camels, are fleet, cursorial types. Thus the physiography of the plains country was varied.

As this is the first glimpse of the life of the great plains of America, it is probable that many of the mammals which are found here were not new to North America, but had been resident on the Great Plains for a considerable period.

Oligocene lizards.[2] — Indications of dry land conditions in the Titanotherium and Oreodon zones of Montana are found in the presence of numerous lizards of a type (*Glyptosaurus*) which has the skull covered with tuberculated bony plates. These animals are referred to the burrowing, nearly limbless family of Anguidæ, and are related to forms also found in the Eocene of the Bridger Formation of Wyoming. In the Oligocene of Nebraska the worm-like, amphisbænian lizards (*Rhineura, Hyporhina*) occur, animals now inhabiting the tropical regions of America and Africa.

In addition to the evidence drawn from geology and the mammals, the

[1] Hatcher, J. B., Origin of the Oligocene and Miocene Deposits of the Great Plains. *Proc. Amer. Philos. Soc.*, Vol. XLI, 1902, pp. 113–131.

[2] Douglass, E., Some Oligocene Lizards. *Ann. Carneg. Mus.*, Vol. IV, nos. 3 and 4, 1908, pp. 278–285.

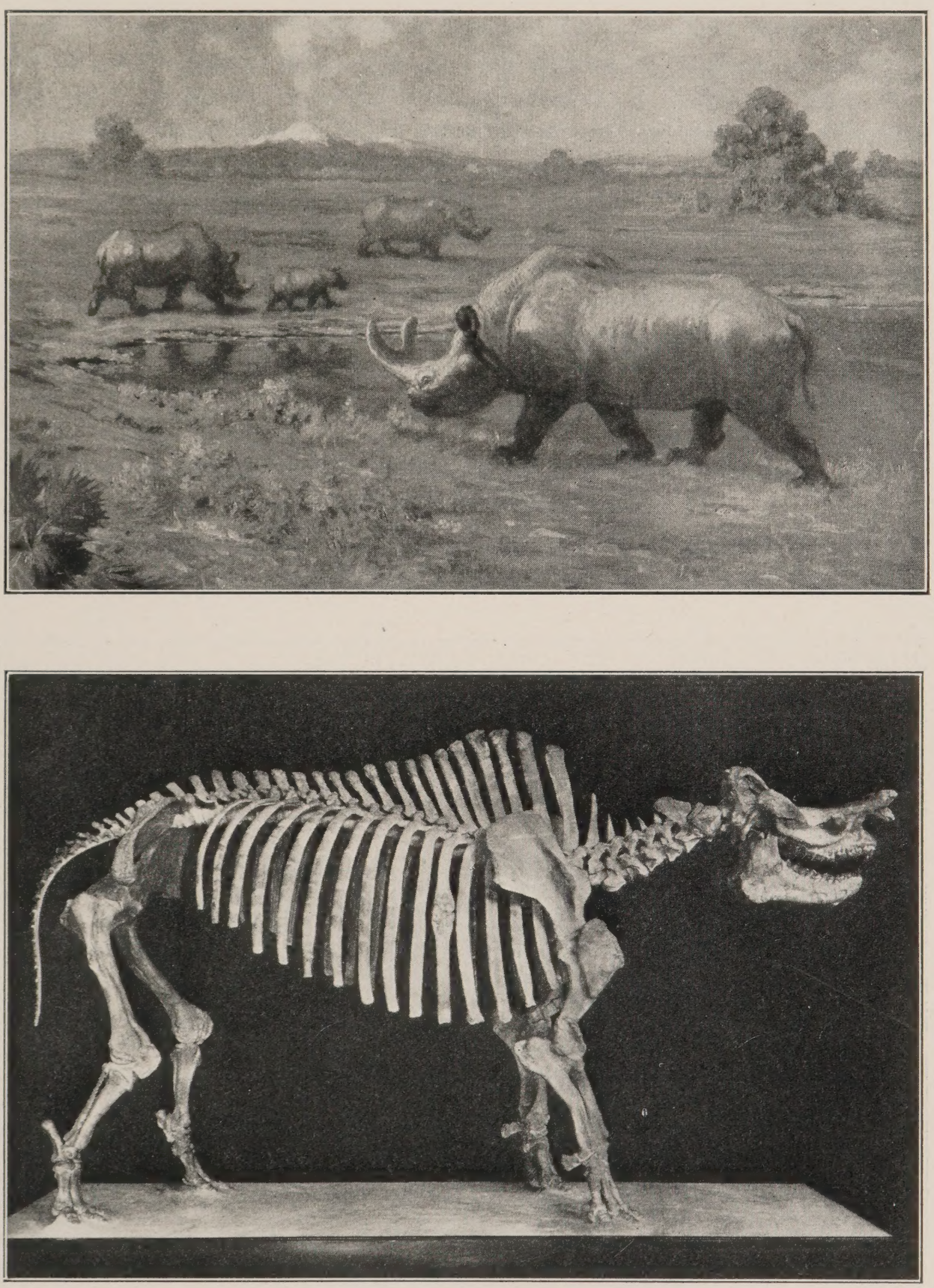


FIG. 97. — Type of the Titanotherium Zone, Lower Oligocene. Above: Herd of titanotheres of the genus *Brontotherium* on an ancient flood plain in the South Dakota region. After original by Charles R. Knight. Below: Skeleton of the giant titanothere *Brontotherium gigas* (female). Both in the American Museum of Natural History.

tortoises (Testudinata), as analyzed by Hay,[1] furnish important proof of prevailing dry land conditions on the great plains. How long previously such conditions had set in it is impossible to say. In the entire Oligocene and Miocene beds of the great plains only six species of water-living turtles have thus far (1907) been recorded, and these are probably from river channel sandstones, as contrasted with a very much larger number of land-living tortoises, chiefly from fine clay deposits. The upland testudinates include in the White River group (Lower to Upper Oligocene) eight species of land tortoises (*Stylemys, Testudo*). Remains of crocodiles have been recorded (Loomis) [2] in river channel beds of Lower Oligocene age.

Physiographic conditions. — The general conditions of Oligocene life in the plains region have already been pictured in the early part of this chapter (p. 179), and we may now review the characters of each subdivision of the Oligocene more in detail.

Lower Oligocene, Lower White River, or Chadron Formation, Titanotherium Zone

This takes us at once into one of the grandest and most famous of mammal-bearing horizons, the 'Titanotherium Beds' of Leidy and Hayden,

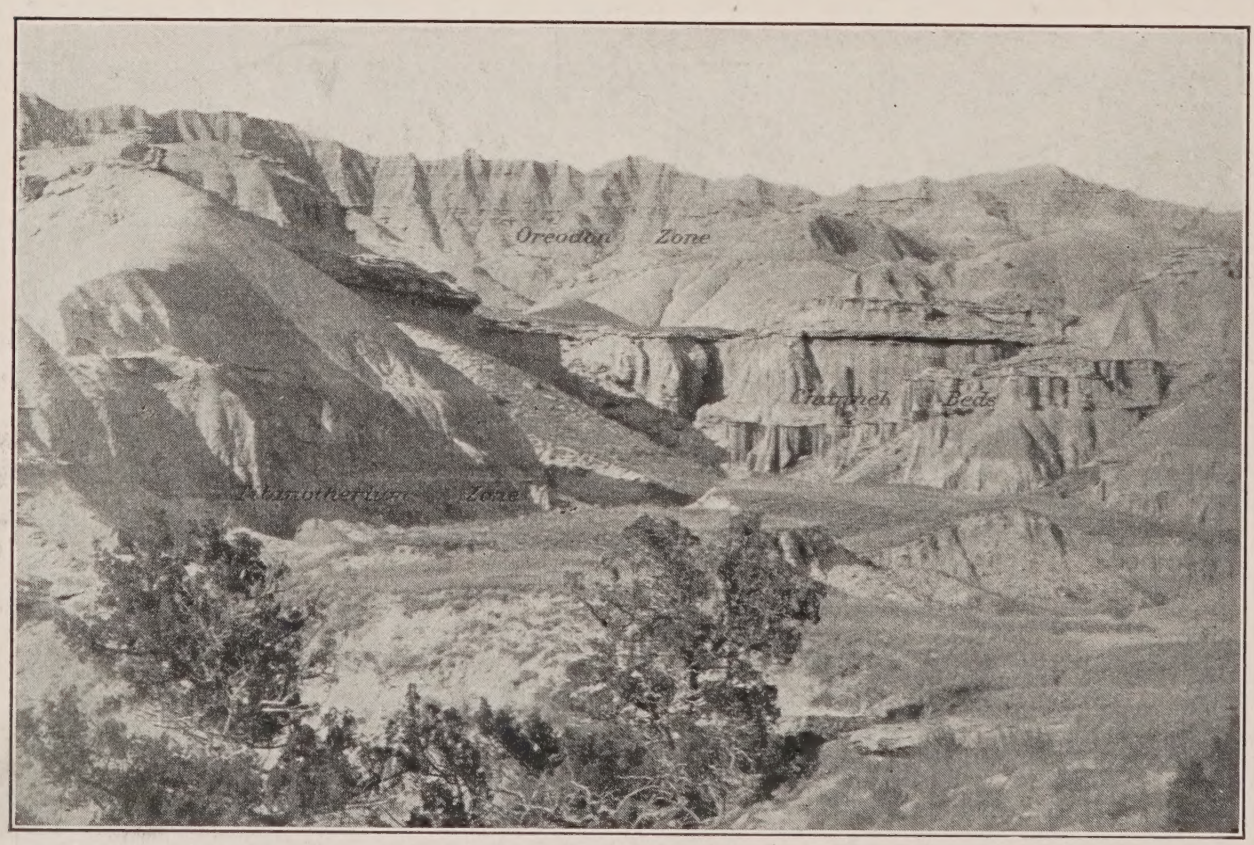
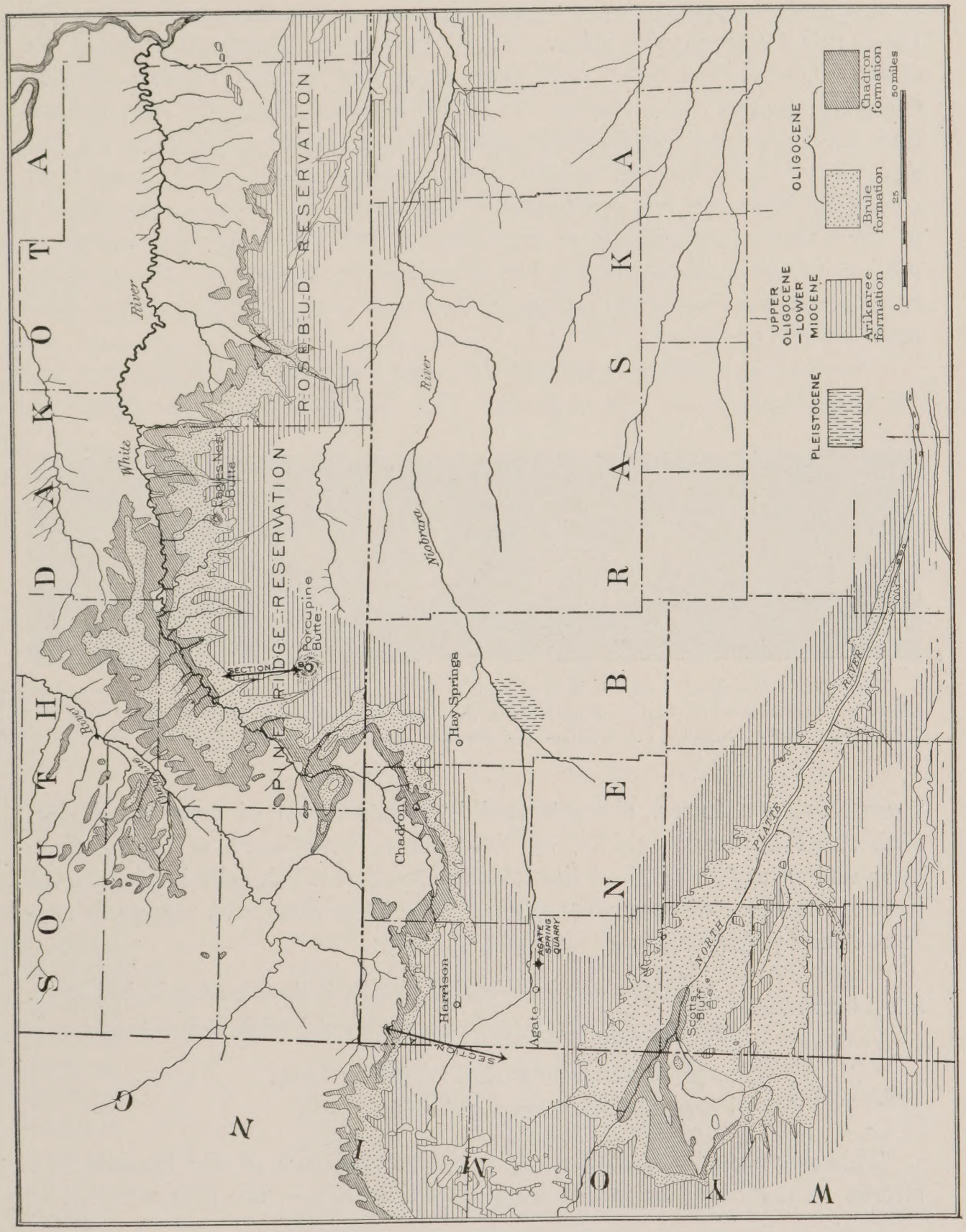


Fig. 98. — In the 'Big Badlands' of South Dakota; Lower and Middle Oligocene. Lower: Titanotherium Zone including channel beds, a river formation. Upper: Oreodon Zone, a flood-plain. Photograph by American Museum of Natural History, 1907.

[1] Hay, O. P., The Fossil Turtles of North America. *Publ. Carneg. Inst.*, Washington, no. 75. 4to, 1908.

[2] Loomis, 1904, *op. cit*



By permission of the U.S. Geological Survey.

FIG. 99. — Oligocene, Lower Miocene and Pleistocene exposures of South Dakota, Nebraska, and eastern Wyoming. After Darton and Thomson. Oblique lines = Titanotherium Zone, Chadron Formation. Dots = Oreodon and Leptauchenia Zones, Brule Formation. Horizontal lines = Promerycochœrus and Merycochœrus Zones, Arikaree Formation. Vertical lines = Pleistocene. Extensive Upper Miocene and Pliocene exposures omitted.

at the very base of the Oligocene, which rest directly upon the irregularly eroded surfaces of the Upper Cretaceous. As shown in the accompanying map, this Chadron Formation (black lines) was widely distributed in South Dakota, Nebraska, and Wyoming, and extends up into British Columbia to the Swift Current Creek Formation. Again in Montana we find the Pipestone Creek, first explored by Douglass,[1] which yields the mammals of smaller size, or microfauna.[2] Since the Titanotherium beds of the Big Badlands are mostly coarse and largely fluviatile, our knowledge of the American mammals of this stage is still rather limited except as regards the titanotheres, which are magnificently represented and undergo their entire final evolution and extinction in this short period of two hundred feet of deposition.

The first to thoroughly explore this zone was Hatcher,[3] while searching for titanothere skulls and skeletons. In 1893 he divided the zone into

FIG. 100. — Heads of Lower Oligocene titanotheres. Representing four contemporaneous phyla, or lines of descent of (*A*) *Megacerops*, (*B*) *Titanotherium*, (*C*) *Symborodon*, (*D*) *Brontotherium*. After originals by Charles R. Knight in the American Museum of Natural History.

three levels: a lower, characterized by titanotheres of very small size, with small horns; a middle, by titanotheres with horns of intermediate size; and an upper, by giant titanotheres, some of which exhibit magnificent horns. Osborn [4] subsequently showed that these dominant mammals represent four phyla or grand divisions, namely:

Short-horned	*Titanotherium*, long-headed, slender-limbed, lacking incisor teeth.
	Megacerops, short-headed, stout-limbed, with incisor teeth.
Long-horned	*Symborodon*, smaller, lacking incisor teeth.
	Brontotherium, larger, with incisor teeth.

This polyphyletic character, or adaptive radiation of the titanotheres, affords us a hint as to varied local conditions which are also reflected in

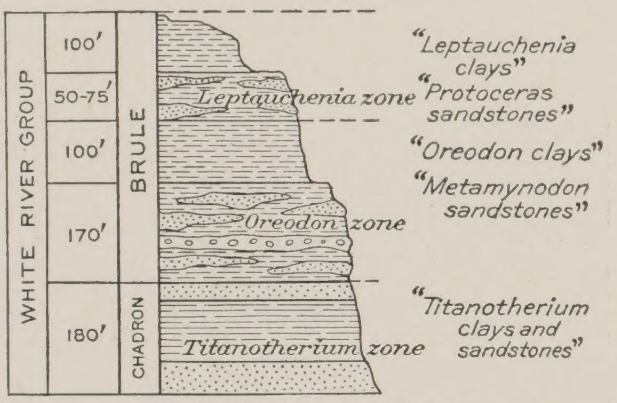
[1] Douglass, Fossil Mammalia of the White River beds of Montana. *Trans. Amer. Philos. Soc.*, n.s., Vol. CC, 1901, pp. 1–42.

[2] *Ibid.*, New Vertebrates from the Montana Tertiary. *Ann. Carneg. Mus.*, Pittsburg, Vol. II, no. 2, 1903, pp. 145–200.

[3] Hatcher, J. B., The Titanotherium Beds. *Amer. Natural.*, March 1, 1893, pp. 204–221.

[4] Osborn, H. F., The Four Phyla of Oligocene Titanotheres. *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI, Art vii, Feb. 18, 1902, pp. 91–109.

the varied structure of the horses. *Titanotherium*, for example, being a slender-limbed, and swift-moving animal, may have cultivated a grazing habit, while *Brontotherium* (Fig. 97) was a heavy-limbed, slow-moving quadruped armed with gigantic horns and teeth of a relatively short-crowned, browsing type. The titanotheres now reach the climax of their evolution and become extinct with apparent suddenness.



By permission of the U.S. Geological Survey.

FIG. 101. — Scale section of the Oligocene White River Group, 'Big Badlands' of South Dakota. After Wortman.

Two members of this family have been discovered in Europe. They are (1) *Brachydiastematherium transsylvanicum* from the vicinity of Andrásháza Klausenburg, Transsylvania, in Hungary, comparable to our *Protitanotherium;* (2) *'Titanotherium' rumelicum* Toula, from Bulgaria. Probably a member of the sub-family Titanotheriinæ (*?Megacerops*).

The faunal group as a whole is exhibited in the following conspectus:

Characteristic Mammals
Opossums
Leptictids
Hyænodonts
True canids
Mustelids
Machærodont cats
Surviving Eocene rodents (ischyromyids)
Heteromyids
Leporids (hares)
Hyracodonts
Amynodonts
Aceratheres
Diceratheres
Lophiodonts
Horses
Chalicotheres
Titanotheres
Entelodonts
Dicotylids
Leptochœrids
Anthracotheres
Camels
Hypertragulids (hornless)

This group seems to be much richer in perissodactyls than that of the Lower Oligocene of western Europe, especially in the presence of the cursorial rhinoceroses or hyracodonts, of the horses, of surviving slender-limbed lophiodonts (*Colodon*), as well as of the great titanotheres. Beside the hyracodont and amynodont rhinoceroses the true rhinoceroses appear, probably both the acerathere and dicerathere ancestors, distinguished (*Trigonias*) by the presence of small upper canine teeth. *Cœnopus* is a still more common form. We note that the artiodactyls are freshly allied to those of Europe through the widespread anthracotheres (*Ancodus ? Anthracotherium*), probably recent arrivals from the Old World. The primitive peccaries (Dicotylidæ), the primitive ruminants (Hypertragulidæ), and the small camels (Camelidæ) are peculiarly American. Primitive insectivores (leptictids and chrysochlorids) occur. The opossums (*Peratherium*) survive. The Carnivora-Creodonta now include a variety of hyænodonts, among which are forms of really gigantic size. The true Carnivora include varied canids (*Daphœnus* and *Cynodictis*), the latter similar

to the Old World form. The light-limbed machærodont, or saber-tooth cats (*Dinictis*) are characteristic, as well as the first mustelids (*Bunælurus*) known in this country.

Every division of the mammals seems to have differentiated into its plains-living and open country types and forest- and river-living types.

FIG. 102. — The Lower Oligocene cursorial rhinoceros *Hyracodon*. After original by Charles R. Knight in the American Museum of Natural History.

Of the former, we observe, among the rodents, the leporids or hares; among rhinoceroses, the light-limbed hyracodonts; among the lophiodonts, *Colodon*. The horses of the period are still polyphyletic, — small, excessively light-limbed, swift animals, models of grace and beauty. Among carnivores, both the canids and machærodont cats are partly cursorial. The scarcely known camels were also plains-living types, although still brachyodont. The peccaries (Dicotylidæ) first appear here.

Of the contrasting forest and lowland fauna, among perissodactyls may be cited the titanotheres, found in the Swift Current Creek deposits of British Columbia. The forest-living tapirs are not known. Among artiodactyls, *Agriochœrus*, a genus of oreodont, also the anthracothere *Ancodus* are probably river-border or forest animals. The amynodont rhinoceroses now take on a distinctly fluviatile, or river-living type; their remains are found only in the river-channel sandstones. Most of the titanotheres were browsers and frequented river borders in the lower plains.

It is striking that no trace of monkeys has been found; in fact, there is every evidence that these animals disappeared from America at or before the close of the Eocene. The small, triangular teeth of *Leptochœrus*, formerly referred to the primates by Marsh and Cope, now prove to belong to a primitive surviving artiodactyl family (Leptochœridæ). Beside the leptochœrids the artiodactyls include the giant pigs or entelodonts, and peccaries or dicotylids, the foreign anthracotheres, and the much more numerous and varied native oreodonts.

FIG. 103. — Skull of the Lower Oligocene titanothere *Brontotherium gigas* (male). In the American Museum of Natural History. After Osborn.

Most important of all, the hypertragulids appear, typified by the diminutive *Hypertragulus* and *Leptomeryx*. The former (*Hypertragulus*) bears some resemblance to the chevrotains (*Tragulus*) of southern Asia. Matthew's recent restudy [1] of *Leptomeryx*, a member of this family, brings

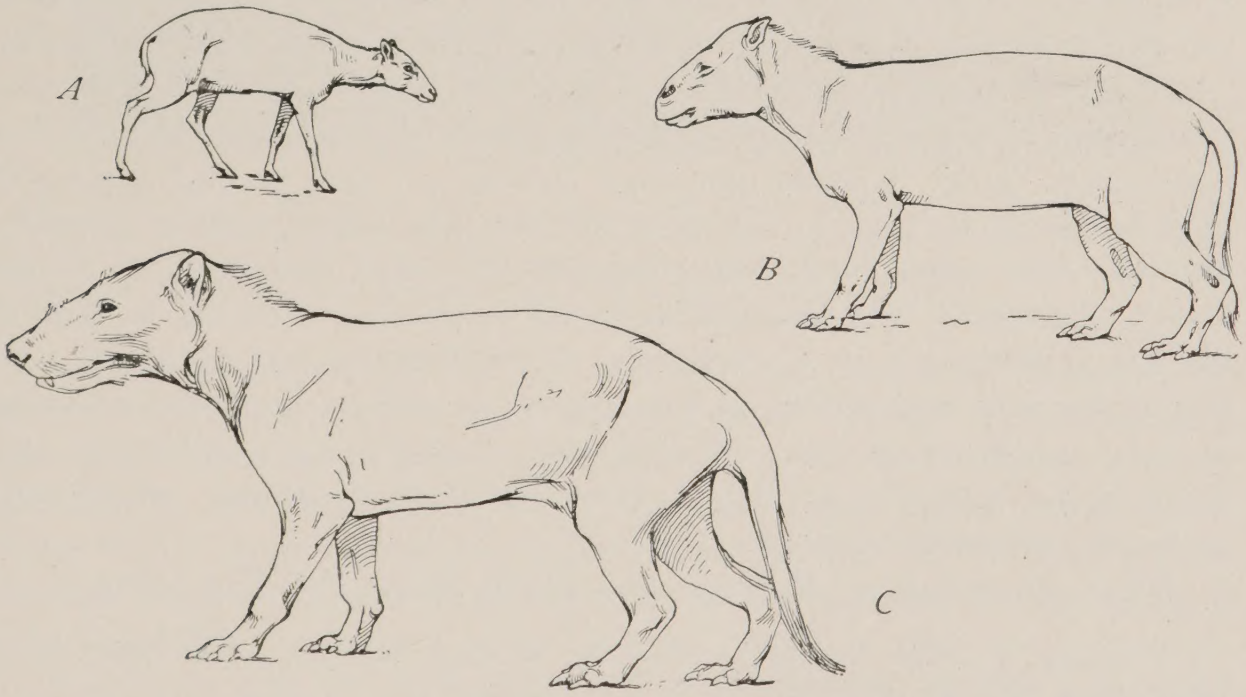


FIG. 104. — Contemporary Lower Oligocene mammals of South Dakota to same scale ($\times \frac{1}{16}$). By Charles R. Knight. *A*. *Leptomeryx*, ancestral hornless deer. *B*. *Oreodon*, a primitive browser or grazer. *C*. *Hyœnodon*, the last of the creodonts.

out the very important fact that it has numerous indications of remote relationship to the true ruminants and especially to the American deer

[1] Matthew, W. D., Osteology of *Blastomeryx* and Phylogeny of the American Cervidæ. *Bull Amer. Mus. Nat. Hist.*, Vol. XXIV, Art. xxvii, 1908, p. 552.

(Cervidæ) rather than to the Old World chevrotains (*Tragulus*) or New World camels (Camelidæ) as had formerly been supposed. Thus in America, as in Europe, there appear in the Lower Oligocene for the first time mammals with a kinship to the cervine or deer division of the ruminants.

In the Pipestone Creek beds of Montana our faunal knowledge has been especially enriched by the discovery and description of the hitherto unknown microfauna of the Titanotherium beds,[1] which includes archaic, tenrec-like forms, as well as erinaceids among Insectivora. These beds belong near the base of the Oligocene (Matthew, p. 201). They contain very primitive insectivores (*Apternodus*) with teeth of ancient type; also a diminutive opossum (*Peratherium titanelix*). All the rodents belong to the ischyromyid and hare divisions. None of the mice or squirrel groups are found here.

Cypress Hills, Saskatchewan. — In 1883 McConnell of the Canadian Survey discovered Tertiary beds in the Cypress Hills, the northernmost mammal-bearing horizons of Tertiary times. As described by Cope[2] (1891) and more fully by Lambe[3] (1908), the fauna is of Lower Oligocene age, corresponding chiefly to that of the Lower Titanotherium beds of Montana, although the upper members may be synchronous with the Oreodon Zone. The formation is fluviatile, or fluvio-lacustrine, and is widely scattered from the Cypress Hills to the Swift Current Creek region. Its fluviatile origin is attested by the presence of abundant remains of fishes, including the bowfins (*Amia*), garpikes (*Lepidosteus*), siluroids (*Rhineastes*). There are also numerous aquatic (*Anosteira, Trionyx*) as well as terrestrial (*Stylemys, Testudo*) chelonians, lizards, snakes, and crocodiles. The mammalian fauna includes opossums (*Didelphys*) and several species of hyænodonts, including one animal of gigantic size (*Hemipsalodon grandis*), also the true canids and machærodonts (*Dinictis*) characteristic of the Lower Oligocene. The mammalian fauna in general is similar to that of the Titanotherium Zone of Nebraska, South Dakota, and Montana. All the titanotheres and several of the equines as well as rhinoceroses belong to very primitive species. Of somewhat doubtful inclusion within this fauna is the supposed ancylopod (*Chalicotherium bilobatum*) which rests upon very uncertain evidence.

White River beds of Montana and North Dakota.[4] — The tertiaries of

[1] Douglass, E., New Vertebrates from the Montana Tertiary. *Ann. Carneg. Mus.*, Vol. II, no. 2, 1903, pp. 145–200.

[1] Matthew, W. D., The Fauna of the Titanotherium Beds at Pipestone Springs, Mont. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX, 1903, pp. 197–226.

[2] Cope, E. D., On Vertebrata from the Tertiary and Cretaceous Rocks of the North West Territory. *Geol. Surv. Canada, Contrib. to Canad. Palæont.*, Vol. III, Montreal, 1891, pp. 1–25.

[3] Lambe, L. M., The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. *Canada Dept. Mines, Contrib. to Canad. Palæont.*, Vol. III, Ottawa, 1908, pp. 1–65.

[4] Douglass, E., A Geological Reconnaissance in North Dakota, Montana, and Idaho; with Notes on Mesozoic and Cenozoic Geology. *Ann. Carneg. Mus.*, Vol. V, nos. 2 and 3, 1909, pp. 211–288.

Montana will be more fully described in the Miocene section (p. 279). The Lower Oligocene beds of White River age overlie the Basal Eocene or Fort Union. They were apparently deposited in streams, lakes, and marshes in ancient river valleys, cut into the Fort Union. Douglass determines beds of both Titanotherium and Oreodon Zones. The Pipestone Creek beds, discovered in 1899, belong in the Titanotherium level, and have yielded a rich fauna of small mammals.

Similarly, in North Dakota there are restricted areas of Lower Oligocene overlying the Fort Union, especially at White Butte, throughout a

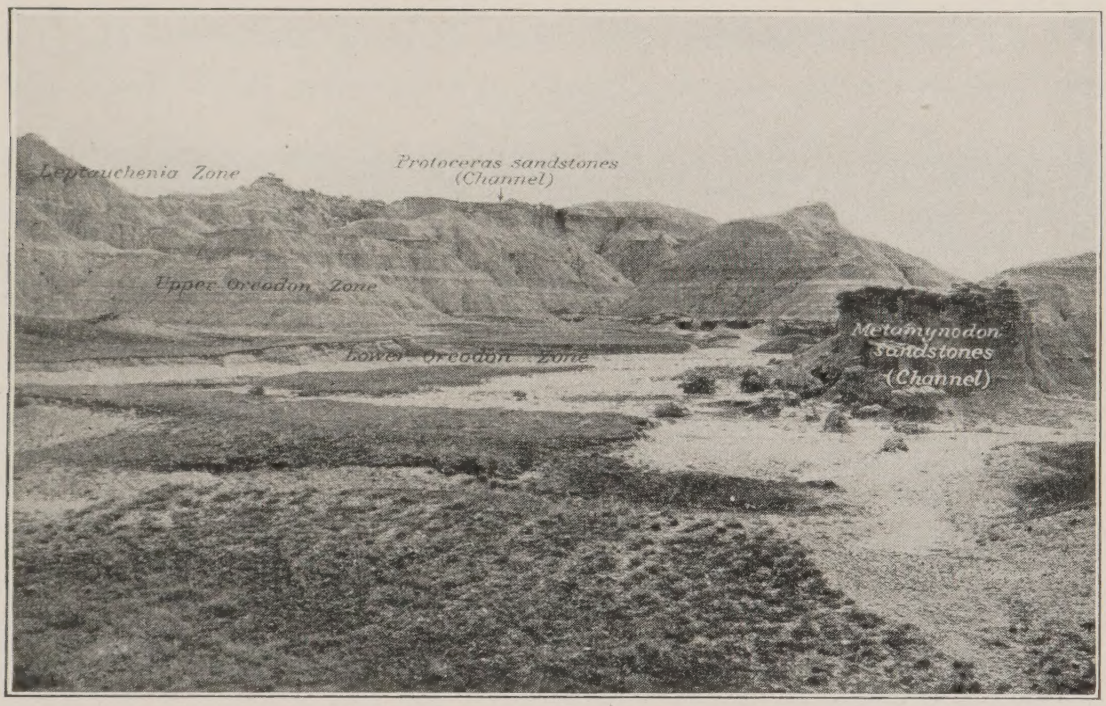


FIG. 105. — 'Big Badlands,' head of Corral Draw, South Dakota. Lower Oreodon Zone, and river channel beds of Metamynodon sandstones in the foreground, overlaid by the Upper Oreodon Zone and capped by the Leptauchenia Zone and river channel beds of the Protoceras sandstones. Photograph by American Museum of Natural History, 1906.

section two hundred and ten feet in thickness, apparently including the Titanotherium Zone below and Oreodon Zone above. Another section affords a thickness of three hundred and twenty feet, which, however, includes the Oreodon and overlying Protoceras and Leptauchenia Zones. These White River formations in North Dakota are believed to represent deposits made in the old river valley traversed by streams originating in the Black Hills.

The giant pigs, or entelodonts. — The family tree of the giant pigs has recently been studied by Peterson,[1] who traces these animals from lower Oligocene ancestors (*Entelodon* in Europe, *Archæotherium* in North America), which may have sprung alike from an unknown northern or Holarctic form. Related, are the Eocene giant pigs (*Achænodon*) of the Washakie and Uinta (Upper Eocene of the Rocky Mountains), too special-

[1] Peterson, O. A., A Revision of the Entelodontidæ. *Mem. Carneg. Mus.*, Vol. IV, no. 3, May, 1909, pp. 41–158, Pls. liv–lxii.

ized in their teeth to be regarded as directly ancestral. The European *Entelodon* of Eymar (1847) or *Elotherium* of Pomel (1847, indet.) is regarded as generically different from the American forms. Of the latter, *Archæotherium* of the Lower Oligocene, Titanotherium Zone, is believed to be distinguished from *Entelodon* by its elongate snout; in brief, its greater dolichocephaly; the earliest phase (*A. mortoni*) gives rise to a series of species, and already in the Upper Titanotherium Zone attains an imposing size (*A. ingens*). The tuberosities of the lower jaw are strongly developed in *Pelonax bathrodon* of the Protoceras Zone, Upper Oligocene. In the Upper Oligocene of the John Day, a massive form, *Boöchœrus humerosus*, appears, distinguished by a long humerus and short feet, a slow-moving type, while the gigantic *Dinohyus hollandi* of the Harrison beds of

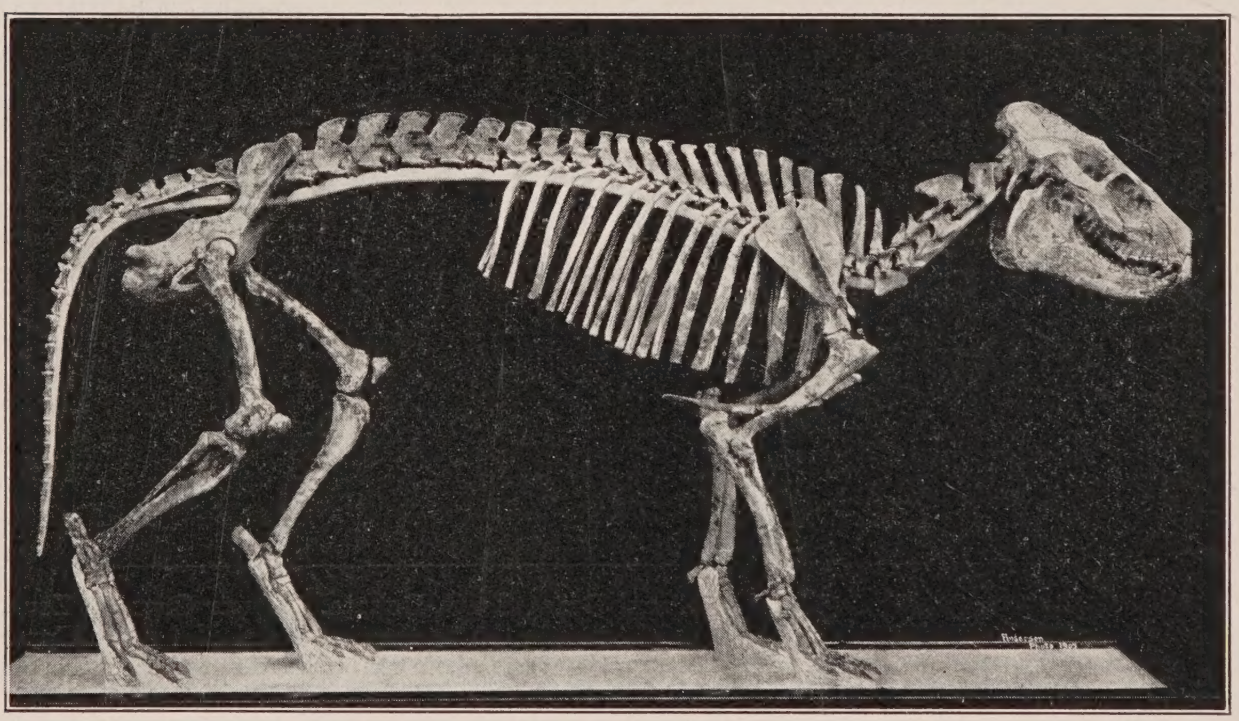


FIG. 106. — Type of the Oreodon Zone. Skeleton of the Middle Oligocene oreodont *Merycoidodon* ("*Oreodon*") *culbertsoni*. In the American Museum of Natural History.

Nebraska is more cursorial. The close of the Oligocene, or beginning of the Miocene witnessed the evolution of four great phyla of entelodonts (*Pelonax*, *Dinohyus*, *Dœodon*, *Boöchœrus*). The distinctions of these phyla require further discrimination.

The geographic range was as far east as New Jersey (*Ammodon* Marsh), while the geologic range is to the summit of the Arikaree beds, which are here regarded as Lower Miocene. It has been suggested by Schlosser and Winge that these animals were omnivorous or even carnivorous, which is highly improbable. The extraordinary appearance, as sketched some years ago under the direction of the present author (Fig. 76), is probably less accurate than the more recent restoration by Mills under the direction of Peterson (Fig. 83), in which the ears are placed lower down and are more drooping, in keeping with the inferior position of the external audi-

tory meatus, which is placed much lower on the sides of the head than in the pigs or peccaries. In Mills' restoration the tuberosities on the lower surface of the jaw represent a mechanism for muscular attachment.

Middle Oligocene, Oreodon Zone or Brule Clays, Stampian Stage

Geology. — Immediately overlying the Titanotherium Zone in the White River Group of the Great Badlands is the Oreodon Zone, or Brule Clays, about 270 feet in thickness, and broadly distinguished as of Middle Oligocene age. While the Titanotherium beds are of colder, grayish tint, these Oreodon layers are warmer buffs and pinks, and, as shown in Fig. 98, are generally distinguished by long, horizontal lines or bands of similar color, which indicate the frequent recurrence of overflow or stillwater conditions. These horizontal bands are an indication of aqueous rather than æolian deposition. Such bands are seldom seen in the Titanotherium Zone of South Dakota, although observed in Titanotherium beds elsewhere. The Oreodon beds are divided by the so-called 'nodular layers' (Fig. 96) into 'Lower,' 'Middle,' and 'Upper,' each with a more or less specific fauna, and affording a series of transitions, including arrivals and departures of animals of different kinds, similar to those which are recorded in the Eocene levels of the Bridger. Thus the Oreodon Zone alone represents a vast interval of geologic time.

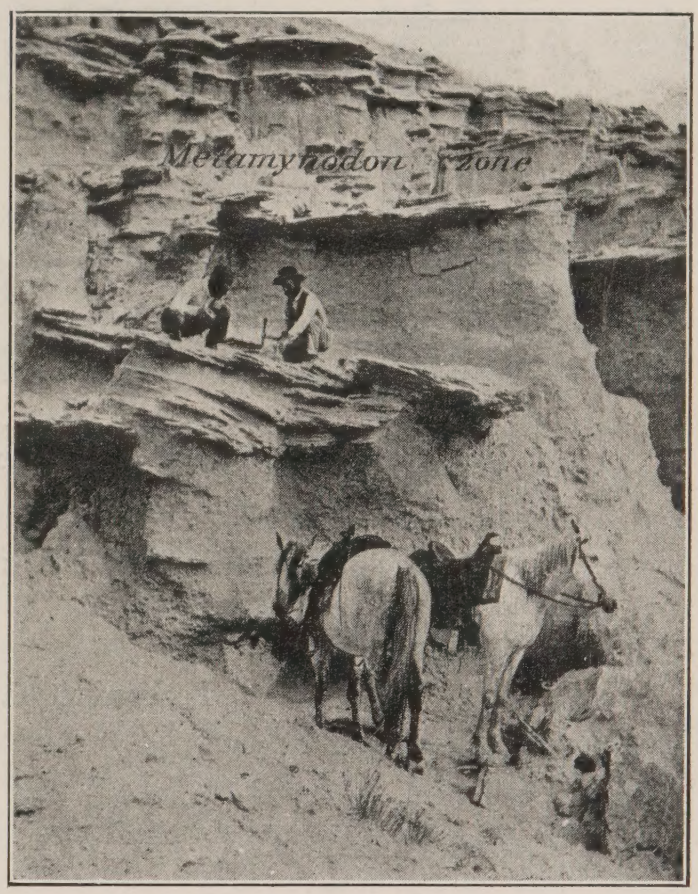


Fig. 107. — Metamynodon sandstones, river channel beds in the Upper Oreodon layers of South Dakota. Photograph by American Museum of Natural History, 1894.

The lower Oreodon Zone is abruptly traversed by the 'Metamynodon Sandstones' (Fig. 105), coarse river channel deposits, cross-bedded sandstones of greenish and brownish color, full of pebbles, containing especially the amphibious rhinoceroses (*Metamynodon*) and other lowland forms. In general, as first observed by Matthew, there is a sharp distinction between the fluviatile and river-border fauna contained in these sandstones

and the plains fauna contained in the clays of the Oreodon Zone.[1] The only explanation is that the clay and sandstone fossils represent two co-existent faunas of different local habitat.[2]

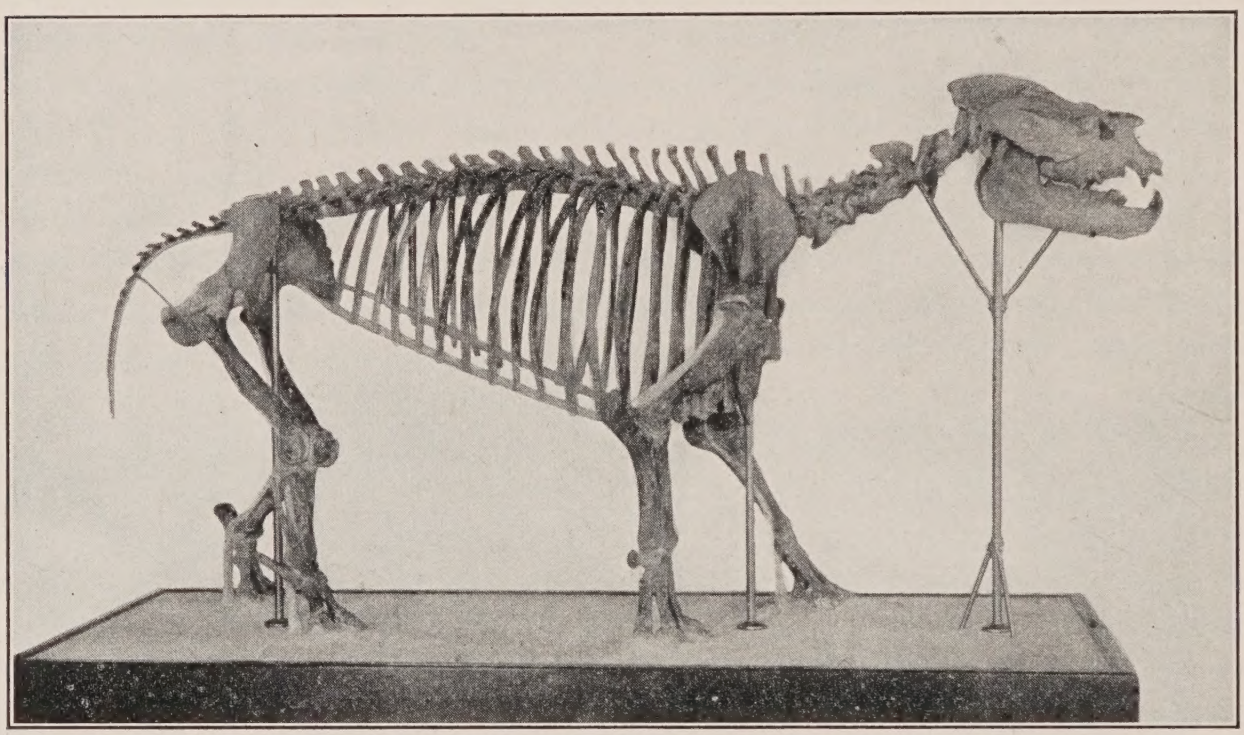


FIG. 108. — Skeleton of the Oligocene aquatic rhinoceros *Metamynodon planifrons*. (See Restoration, page 180). In the American Museum of Natural History. After Osborn.

Contrasting Plains and River-Border Mammals

Chiefly Plains	Chiefly Riverside
Perissodactyla	
Mesohippus bairdi, meteulophus, etc.	*Mesohippus intermedius* and *Miohippus*
Hyracodon	*Metamynodon*
Colodon	*Cœnopus*
	Protapirus
	Titanotherium
Artiodactyla	
Leptauchenia	*Agriochœrus*
Oreodon	*Perchœrus*
Eporeodon	*Entelodon*
Poëbrotherium	*Ancodus*
Leptomeryx	*Anthracotherium*
Hypertragulus	*Protoceras*
Hypisodus	

[1] Matthew, A Provisional Classification of the Fresh-Water Tertiary of the West. *Bull. Amer. Mus. Nat. Hist.*, Vol. XII, 1899, pp. 19–75.

[2] Matthew, Fossil Mammals of the Tertiary of Northeastern Colorado. *Mem. Amer. Mus. Nat. Hist.*, no. 1, Pt. 7, Nov., 1901.

Chiefly Plains	Chiefly Riverside
	Carnivora
Hyænodon	
Dinictis	
Cynodictis	
Hoplophoneus	*Hoplophoneus*
Daphœnus	*Daphœnus*
	Rodentia
Ischyromys	
Palæolagus	*Steneofiber*
Eumys	
Gymnoptychus	
	Insectivora
Leptictidæ	

Of the same age are the 'Cedar Creek' beds of northeastern Colorado and widespread similar exposures in southeastern Wyoming, South Dakota, northwestern Nebraska, and far north in western Montana. These exposures are renewed proofs of the existence of vast fertile and nearly level flood plains, east of the Rockies, gently sloping eastward and traversed by stream channels or rivers which are narrower than those of *Titanotherium* times. The plain is chiefly forested along the river borders; but the flora is entirely unknown.

Approximate homotaxis with the Stampian or Middle Oligocene of Europe is indicated by similar stages in the evolution of the anthracotheres (*Ancodus*), of the amynodont rhinoceroses (*Metamynodon, Cadurcotherium*), of the true rhinoceroses, or aceratheres and diceratheres. In both countries the Middle Oligocene is the disappearing point both of the amynodonts and of the archaic carnivores (hyænodonts).

The Oreodon beds are the favorite fossil hunting grounds of the West, because the fossils are or were extremely abundant. The mammalian fauna is also very rich, more than 150 species of mammals having been found in the Big Badlands of South Dakota alone. Since this level is much more favorable for the smaller forms of life than the Titanotherium Zone, the considerable number of new forms is partly attributable to this fact. Large herds of the small browsing oreodonts took the place of the cænotheres in Europe, and other ruminants abound in this level.

The observer readily distinguishes the *Oreodon* stage not only by its geologic differences, but by the abundance of oreodonts and the absence of all traces of titanotheres. The Rodentia include the tree-living squirrels (*Prosciurus*), the ground-squirrel or semi-cursorial type (*Eutypomys*), and the hares, or leporids (*Palæolagus*); the mice, or Muridæ, now make their first appearance (*Eumys*), while the peculiarly Eocene ischyromyids make their last appearance. Among Insectivora the erinaceids appear for the first time (*Proterix*), and the talpids or moles (*Domnina*), are represented. The opossums appear in numerous species (*Peratherium*).

Among carnivores the archaic hyænodonts also appear for the last time, and are represented by rather highly varied forms, animals dissimilar in size, speed, and in the proportions of the skull, ranging from the diminutive *H. mustelinus* to the powerful *H. horridus* (Fig. 81), and including also species (*H. leptocephalus*) which exhibit in the closure of the posterior palate a backward extension of the respiratory tract which has been regarded (Scott) as evidence of aquatic adaptation,[1] but may be correlated with the extreme posterior position of the cutting or sectorial molars. At the same time the machærodont cats specialized into the fleet and slender-limbed, swift-moving *Dinictis* and the heavy-limbed *Hoplophoneus* (Fig. 87), which is transitional to the *Eusmilus* of the Upper

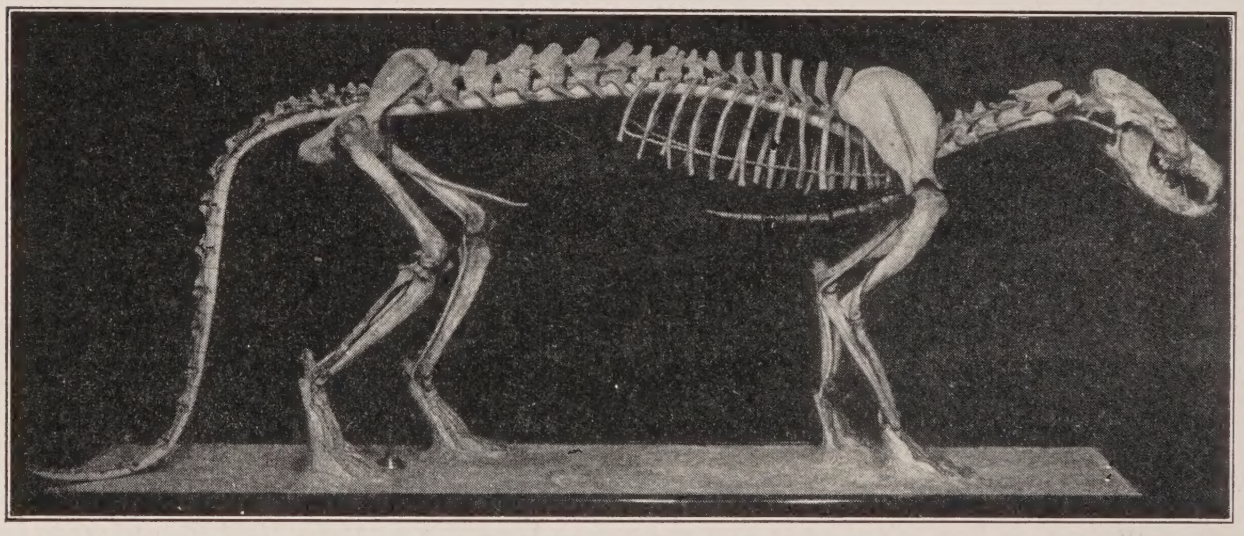


Fig. 109. — Skeleton of the Oligocene wolf, *Daphænus*. In the Carnegie Museum, Pittsburg. After Peterson.

Oligocene. The canids [2] also vary widely from the small civet-like *Cynodictis* to powerful forms such as *Daphænus nebrascensis*, which equaled the wolf (*Canis lupus*) in size.

The Herbivora which formed the prey of these carnivores are included in six families of artiodactyls and six families of perissodactyls, these two orders at the time being nearly balanced both in numbers and differentiation. Of the artiodactyls the camelids (*Poëbrotherium*), which are now of slender form, begin to take a prominent part in the Plains fauna. The hypertragulids, or primitive ruminants and deer, are still diminutive and hornless forms. The oreodonts are of intermediate size and now more sharply differentiated into three phyla, (1) the small brachycephalic *Leptauchenia* being added to (2) the typical cropping or grazing oreodonts and to (3) the forest-living *Agriochœrus*. Diminutive also are the leptochœrids. Of intermediate size are the anthracotheres, which include both the *An-*

[1] Scott, W. B., and Osborn, H. F., Preliminary Account of the Fossil Mammals from the White River Formation, contained in the Mus. Comp. Zoöl. *Bull. Mus. Comp. Zoöl., Harvard Coll.*, Vol. XIII, 1887, pp. 152 fol.

[2] Hatcher, J. B., Oligocene Canidæ. *Mem. Carnegie Mus.*, Vol. I, Sept., 1902.

codus and *Anthracotherium* of European origin; the anthracotheres exhibit no tendency to attain the great proportions displayed in the European and Asiatic forms. Of the pig-like forms the peccaries (*Perchœrus*) are less numerous than the entelodonts; the latter now begin to attain giant size (*E. ingens*), thus assuming a rank similar to that of the anthracotheres in Europe.

The perissodactyls are similarly differentiated into the massive river-frequenting amynodonts (*Metamynodon*) with hypsodont molars and power-

FIG. 110. — The Lower Oligocene three-toed horse *Mesohippus*, a swift, light-limbed animal. To the right *Dinictis*, the light-limbed saber-tooth cat. After original by Charles R. Knight in the American Museum of Natural History.

ful canine tusks, and the extremely long-limbed, long-footed, but still tridactyl lophiodonts (*Colodon*); these lophiodonts are of considerably larger size than the contemporary horses. From the Oreodon Zone comes the typical *Mesohippus bairdi* of Leidy, an extremely light-limbed equine, and there now is becoming more apparent the incipient adaptive radiation of the horses into forest-living and browsing types (*Mesohippus eulophus*, remotely related to the forest-living horse, *Hypohippus*, of the Miocene), and plains or grazing types (*M. obliquidens*). Some of these horses are chiefly found in the 'Clays' (*M. eulophus*, *M. bairdi*, *M. obliquidens*), others chiefly occur in the 'sandstones' of this and higher levels (*M. intermedius*, *M. validus*, *M. gidleyi*). The tapirs (*Protapirus*) are rare. The fleet-footed cursorial rhinoceroses, or hyracodonts, are numerous and characteristic of this horizon. As in Europe the true rhinoceroses are clearly divided into the dicerathere, or two-horned, and the acerathere, or hornless, series.

Upper Oligocene of the Western Plains and of the Mountain Region of Oregon

The Upper Oligocene of America broadly corresponds to the close of the Stampian and the Aquitanian stages of Europe. In both countries it is characterized negatively by the absence of the hyænodonts, the last of the archaic Mammalia, as well as of the amynodonts or amphibious rhinoceroses. Especially characteristic are various evolution stages of the pair-horned rhinoceroses (*Diceratherium*), which are now armed with a transversely placed pair of horns on the ends of the nasal bones. Another common form which makes its first appearance in both the New and Old Worlds at this time is the primitive beaver or castorid (*Steneofiber*).

It is difficult, however, to draw close time parallels between Europe and America because of new and plainly evident faunal divergence. Of the six families of American artiodactyls only the anthracotheres are represented in Europe, and that by very different forms from those in America. Of the four families of American perissodactyls both the hyracodonts and the horses are absent in Europe, although the rhinoceroses and tapirs are represented by somewhat similar evolution stages. Of the ancylopods, or chalicotheres, the *Moropus* of Oregon still awaits close comparison with the *Macrotherium* of France; the wrist, or carpus, of *Moropus* is the more primitive.

The Upper Oligocene of western America is clearly divided into Early, Middle, and Later, or first, second, and third faunal phases, the former being seen in the upper levels of the White River group of Dakota, which contain a continuation of the Plains fauna, while the second, as displayed in the John Day Valley of Oregon, gives us a renewed glimpse of the mountain fauna and corresponds most closely with the true Aquitanian of France. The third is again observed on the Great Plains of Dakota, is slightly subsequent to St. Gérand-le-Puy in age, and is by many regarded as the base of the Miocene.

Third Phase. — Upper John Day of Oregon. Lower Harrison, Rosebud, and Arikaree of the Great Plains of Dakota.	Diceratheres very numerous. *Promerycochœrus* appearing.
Second Phase. — Middle levels (Diceratherium Zone) of the John Day Formation of Oregon.	Diceratheres with well-developed horns. Chalicotheres in the *Moropus* stage.
First Phase. — Upper part of White River Group of South Dakota, Leptauchenia and Protoceras Zones.	Diceratheres with very rudimentary horns. *Cynodictis* and *Hyracodon* still surviving. *Leptauchenia.*

First Phase of the Upper Oligocene, Leptauchenia–Protoceras Zone

Geologic conditions. — The upper part of the Brule Clays of the White River Group in the Great Badlands immediately and conformably overlie the Oreodon Zone. Correlated with these are widespread deposits in northeastern Colorado and in North Dakota, indicating a continuation of

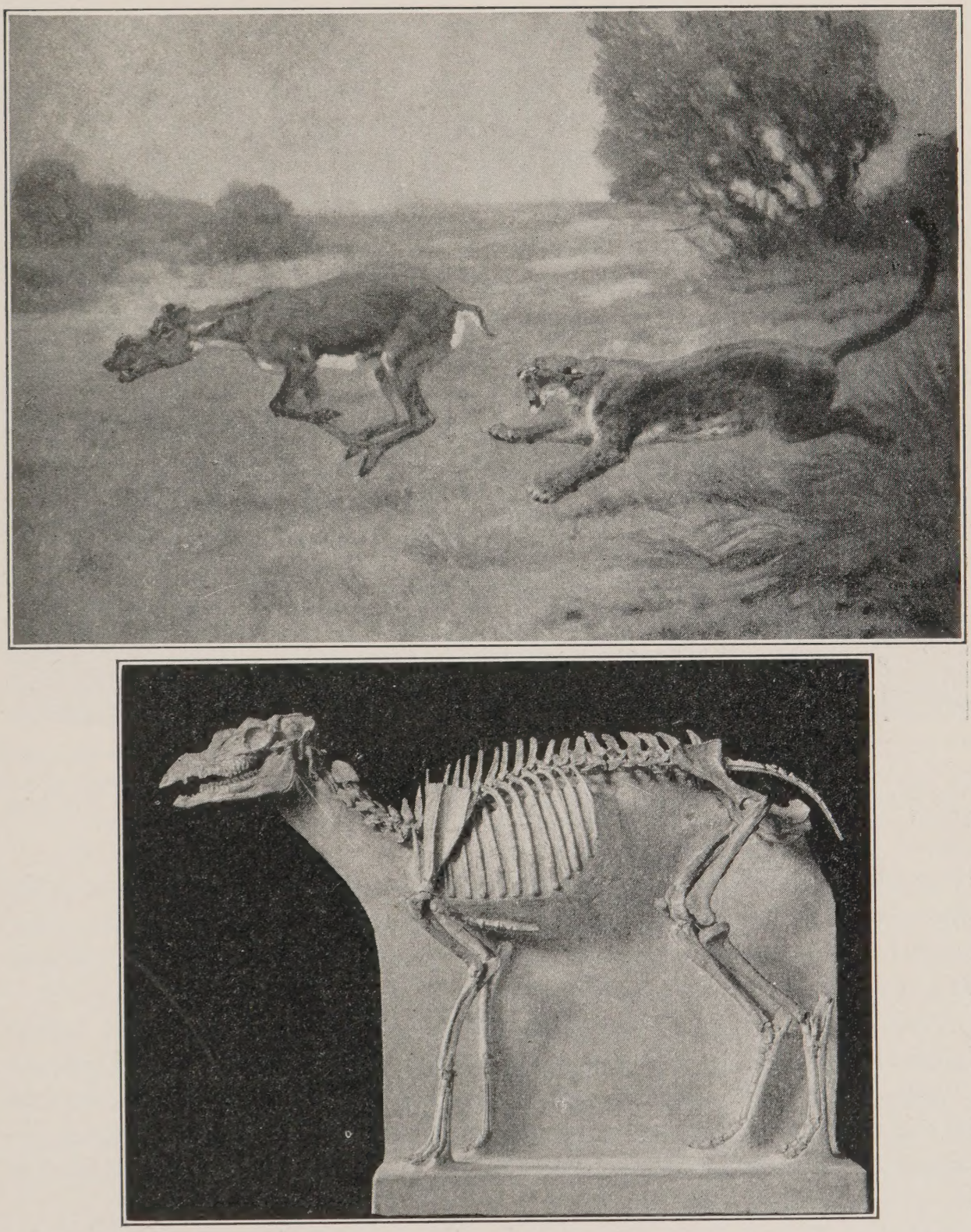


FIG. 111. — The Upper Oligocene four-horned ruminant type of the Protoceras Zone. Above : *Protoceras* chased by the light-limbed saber-tooth *Dinictis*. After original by Charles R. Knight. Below : Skeleton of *Protoceras celer*. Both in the American Museum of Natural History.

the wide flood plain conditions. A similar fauna (*Leptauchenia*) was apparently partly contained in the lower part of the John Day Formation of Oregon, in which, however, fossils are so scarce that reference to the Leptauchenia Zone is provisional. In contrast with the underlying Oreodon beds the 'clays' are relatively barren. The sparsely preserved plains mammals of the period are contained in the upper part of the Brule Clays or so-called Leptauchenia Zone, while the forest and fluviatile mammals are found in relative abundance in the Protoceras sandstones, old river

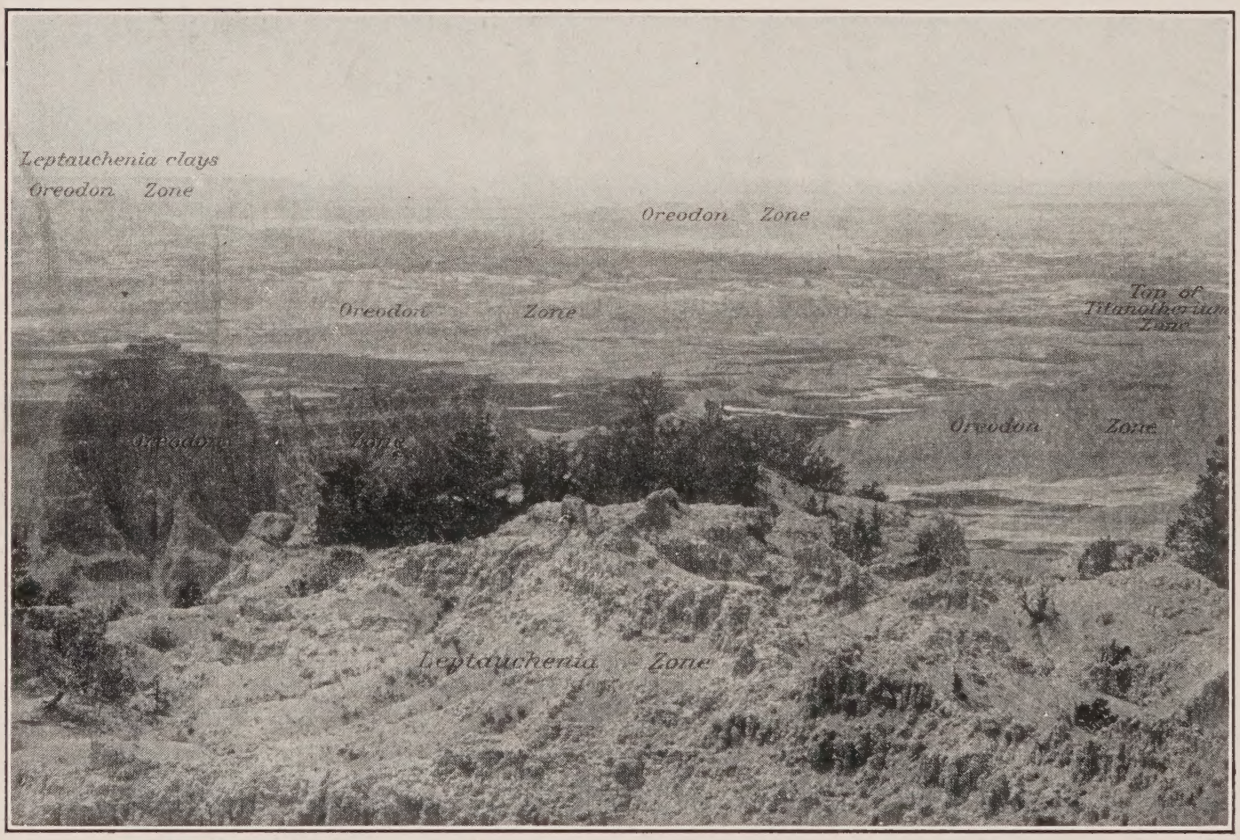


FIG. 112. — Panorama from the summit of Sheep Mountain, South Dakota, an eroded area of the Upper Oligocene. Leptauchenia Zone in the foreground, the underlying Oreodon and Titanotherium Zones appearing in the distance. Photograph by American Museum of Natural History, 1904.

channels of brilliant greenish tint which traverse different levels of the finer buff and pinkish deposits of the Clays. Vertical or 'organ pipe' erosion of these 'clays' is very characteristic. Whitish layers of volcanic ash occur, and very few fossils are found.

Remains of mammals are altogether far more scarce than in the underlying Oreodon Zone, being confined to 21 species. Of these the chief new member is the castorid (*Steneofiber*) which makes its first appearance here in the form of a very primitive species, *S. nebrascensis*. This animal becomes of decided chronologic value in its subsequent evolution because of its wide geographic distribution.

Highly characteristic of and giving the name to the sandstones is the remarkable artiodactyl *Protoceras*, an animal of the height of the sheep, remotely related to the American deer and to the hypertragulids, but not

descended from any known American ancestor, therefore probably a newcomer; it exhibits two pairs of short, plated or rounded, bony horns, or bosses, and canine tusks like those of the muntjacs. In these sandstones was discovered also the finely preserved dicerathere *Cœnopus tridactylus*, a descendant of the *Cœnopus occidentalis* of the Oreodon Zone, in which paired rugosities on the nasal bones of old male specimens are prophetic of the prominent horns of the later *Diceratherium*. In the same sandstones are found tapirs (*Protapirus validus*) of larger proportions, and small-headed horses (*Mesohippus intermedius*) of considerably larger size, which more nearly approach the *Anchitherium* type of the Lower Miocene of Europe; in fact, the six species of horses found on this level represent a great advance upon those of the Oreodon Zone. Three of these species pass into the higher *Miohippus* stage of the Upper Oligocene, or John Day. Among Carnivora it is noteworthy that *Cynodictis* survives and that the machærodonts now include *Eusmilus*.

The adaptive radiation into plains and lowland mammals beginning in the Titanotherium and Oreodon Zones is thus still more strongly marked, but the plains types are relatively little known. Among artiodactyls, the entelodonts, peccaries, anthracotheres, oreodonts, hypertragulids, and camelids are all represented, the latter passing into the somewhat more advanced side branch of camel development known as *Pseudolabis*.

Second Phase of the Upper Oligocene, Diceratherium Zone

John Day Formation of Oregon. — This grand formation carries us for the first time into the mammal life of the extreme northwestern states, which has become known through the successive explorations and researches of Condon, Sternberg, Wortman, Cope, Merriam, and Sinclair.[1] We owe the discovery of these beds to the veteran geologist of Oregon, Professor Condon. It is a sharply defined volcanic deposition of a total thickness of 1,650 feet, composed of tuffs, divided into lower, middle, and upper levels by two rhyolitic flows, and sharply bounded at the summit by a gigantic basaltic outflow two thousand feet in thickness, known as the Columbia River Lava, which is regarded as of Lower Miocene age. As described by Merriam,[2] the volcanic materials of the John Day deposits were chiefly wind-blown, or æolian. There is little evidence of fluviatile conditions. The greater portion of the series is presumably made up of slow accumulations of ash which fell mainly on open plains, upon which shifting, shallow lakes may have existed from time to time. The John Day beds show a remarkable evenness in their strati-

[1] Principal titles given in Bibliography.

[2] Merriam, J. C., A Contribution to the Geology of the John Day Basin. *Univ. Cal., Bull. Dept. Geol.*, Vol. II, 1901, p. 269 fol.; and, Carnivora from the Tertiary Formations of the John Day Region. *Univ. Cal., Bull. Dept. Geol.*, Vol. V, 1906, pp. 1–64.

fication. In the latter part of the period the topography appears to have been more diversified and the action of streams to have become more pronounced (p. 3). The Mollusca are terrestrial, or air breathing types, with the exception of those of one locality, which are fluviatile. The Testudinata (genus *Stylemys*) are of the *Testudo* or terrestrial type, no river-living turtles having been recorded; neither is there any evidence of crocodiles. Even the so-called beavers (Castoridæ) are of the genus *Steneofiber*, not a true river-living form. This time-keeping rodent (see

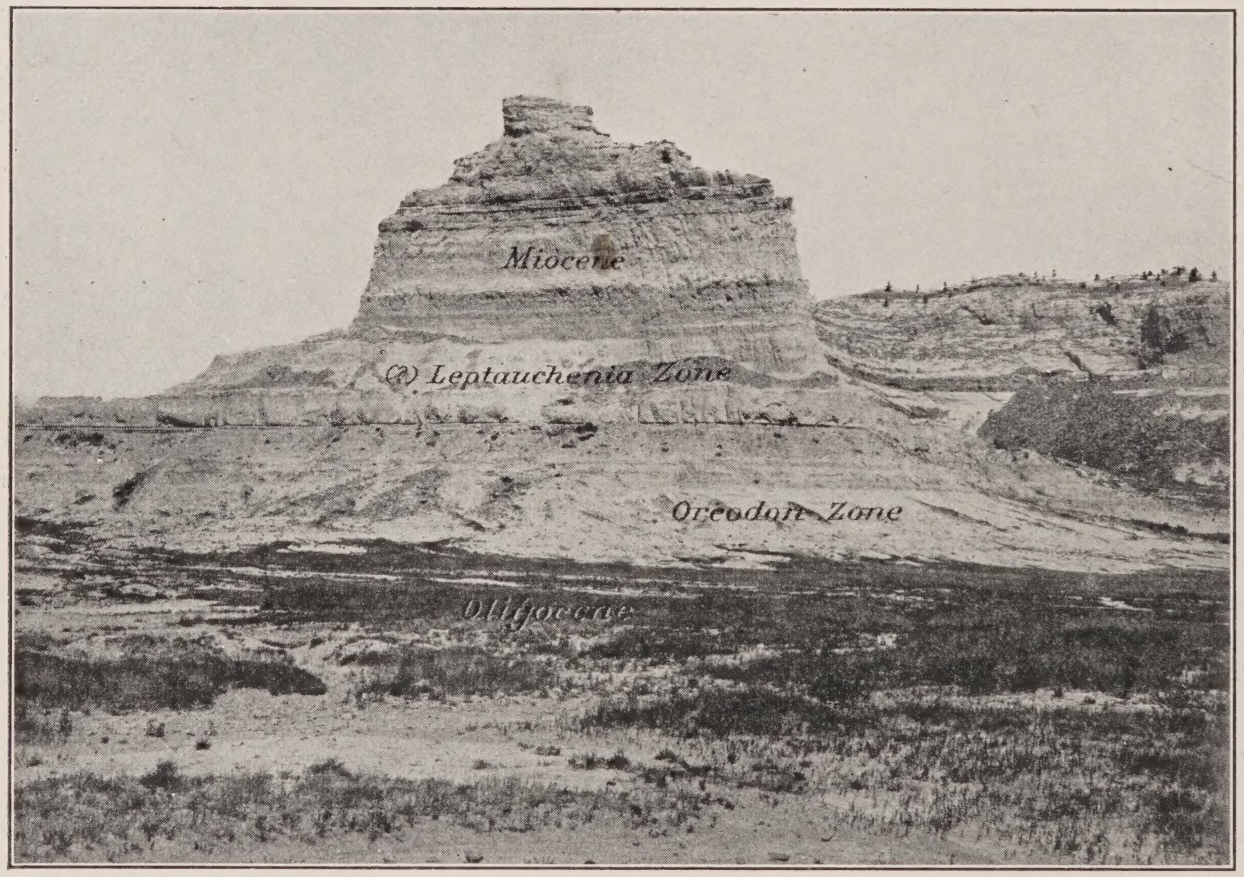


Fig. 113. — View of Scott's Bluff, a famous landmark in western Nebraska. Upper Oligocene of the Oreodon and supposed Leptauchenia Zones, overlaid by Miocene. Photograph by American Museum of Natural History, 1908.

p. 197), it may be observed parenthetically, is in the same stage of evolution as its relatives in St. Gérand-le-Puy of France. The remains of forests are found in the middle of the tuff deposits, and the great forest at the summit was overtaken and submerged by the lava flow, the trunks of the trees still standing.

The known mammalian fauna of the John Day Formation is chiefly of the open-forest, river-border, and savannah-living type. Brachyodont or browsing types of molar teeth still prevail. The beginning of this great deposition in the John Day valley of Oregon appears to correspond very nearly with that of the closing deposition of the White River group, Brule Clays, or Leptauchenia Zone of the Dakota region just described; but the mammals of these beds are so sparse and little known that few deduc-

tions can be made from them except that they are closely related to those of the overlying 'Middle John Day.'

Our full knowledge of the mammalian life of this great basin, therefore, begins with the richly fossiliferous levels of the Middle John Day, or Diceratherium Zone, which contains a varied mammalian fauna considerably more advanced than that of the Leptauchenia-Protoceras Zones, above described, and, as pointed out by Scott, on the whole closely similar in its evolution to the St. Gérand-le-Puy fauna of France. One hundred species of mammals have been described from this level, and while this

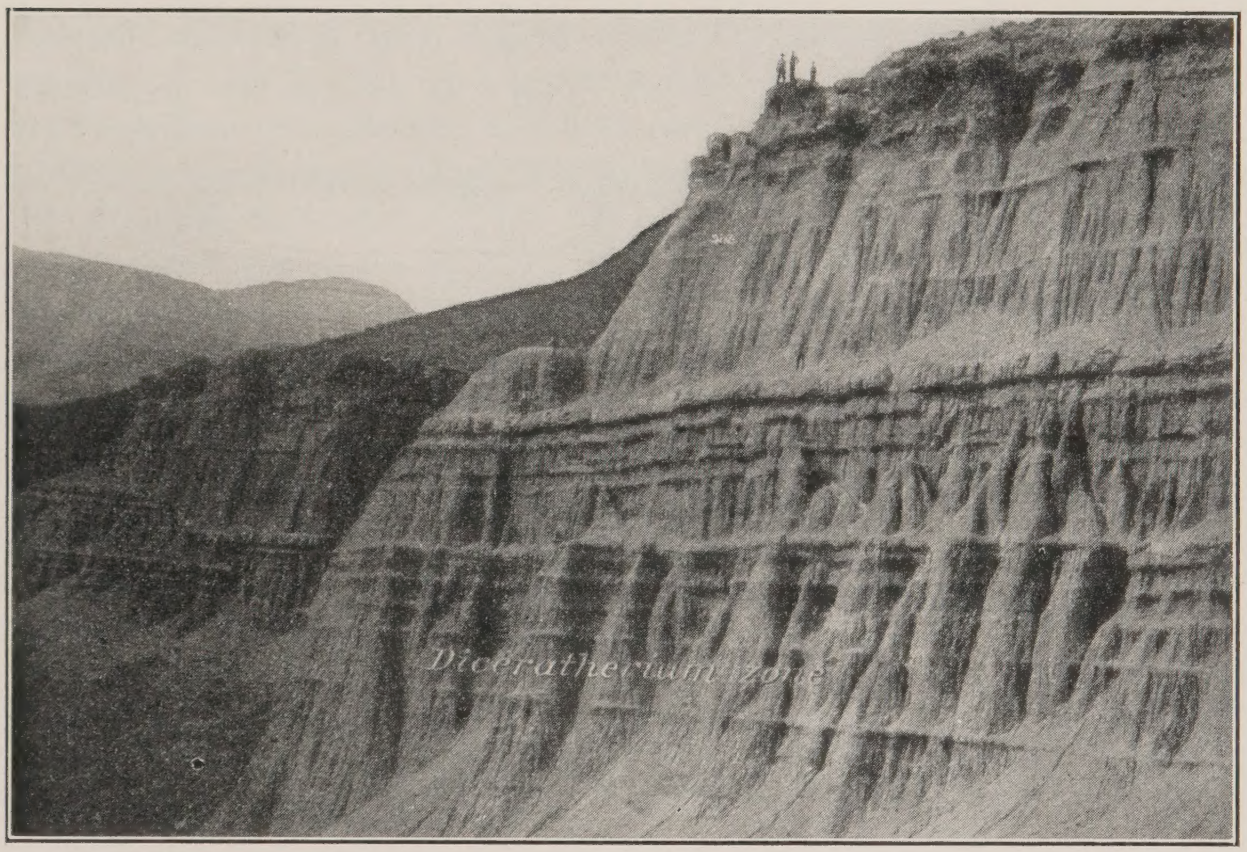


FIG. 114. — Middle John Day Formation, Oregon; Diceratherium Zone. Photograph by University of California, 1900.

list may be reduced by closer comparison, it also will be expanded by further exploration. As in the Upper Oligocene of France we note the entire disappearance of the archaic hyænodonts; among rhinoceroses the cursorial hyracodonts are absent; among Artiodactyla no traces have been found of the primitive family of leptochœrids, nor of the anthracotheres; among smaller mammals it is noteworthy that there are no traces of the opossums (didelphyids).

Among rodents we note the reappearance of the castorid *Steneofiber*, first observed in the somewhat older Protoceras Zone, and also highly characteristic of the European Upper Oligocene. Still more striking is the first appearance of the peculiarly American haplodontids or sewellels, which even at the present time are confined to the Rocky Mountain region. These animals (see p. 534) are sciuromorphs, remotely related to the Eocene

and Lower Oligocene ischyromyids of North America. Noteworthy also is the first appearance of the geomyids, or pocket gophers, another rodent family which is peculiar to North America. Besides these castorids, gophers, sewellels, and sciurids, there are murids and leporids, the last family including a species actually referred to the existing genus *Lepus*.

The perissodactyl ungulates are now reduced from seven families to the three existing families of Equidæ, Tapiridæ, and Rhinocerotidæ, and the extinct aberrant family of Chalicotheriidæ. Among the rhinoceroses the diceratheres are in a much more advanced stage of evolution than in the Protoceras or Leptauchenia Zone, as they exhibit a pair of well-developed horn cores upon the nasals (as in the *D. minutum* of Moissac, France), and include animals of a considerable range in size. These pair-horned rhinoceroses are especially numerous and characteristic. Aceratheres have not been recognized in the Oregon region, although they were undoubtedly present. Among the tapirs, *Protapirus* is similar to that found in the *Protoceras* sandstones of the White River group, a single species, *P. robustus*. The horses are numerous; they present a slight advance upon those of the Protoceras sandstones, and are now chiefly referred to the stage *Miohippus*, while one species (*A. præstans*) from the Upper John Day is very similar to the Lower Miocene *Anchitherium* of Europe. The chalicotheres are represented by three species in the *Moropus* stage of evolution.

The Carnivora [1] are confined to the three families, canids, mustelids, and felids. Of these the dogs still include *Cynodictis* (Merriam) beside a great variety of more modern genera (*Nothocyon, Mesocyon, Temnocyon*, a descendant of *Daphœnus, Paradaphœnus, Enhydrocyon, Philotrox*). This is the most remarkable assemblage of canids known in any formation in America. Beside the long-faced dogs (*Temnocyon*) there were short-faced forms (*Enhydrocyon, Philotrox*), analogous to the *Simocyon* type of Europe. *Oligobunis* was formerly considered a dog; it is now regarded as a mustelid. The felids also indicate that during the deposition of the Middle John Day the region included a country of open savannahs favoring the running types. The mid-Oligocene separation observed by Matthew [2] between (1) the *Dinictis* phylum, which is more truly feline, and (2) the *Hoplophoneus* phylum, which is more truly machærodont, is now indicated by the light-limbed *Nimravus*, and the machærodont *Hoplophoneus*, which still survives.

Of the Artiodactyla, five families are known, namely: entelodonts, dicotylids, oreodonts, hypertragulids, and camelids. The entelodonts begin to approximate the climax of their evolution, including animals of massive size and robust limbs (*E. imperator*), and a considerable variety

[1] Merriam, J. C., Carnivora from the Tertiary of the John Day Region. *Univ. Cal. Publ., Bull. Dept. Geol.*, Vol. V, no. 1, 1906, pp. 1–64.

[2] Matthew, W. D., Fossil Mammals of the Tertiary of Northeastern Colorado, 1901, pp. 387–394.

of specific forms. Similarly the suillines, or dicotylids, are found in great numbers (*Perchœrus*) and in a variety of specific forms. Of the oreodonts the *Agriochœrus* phylum reaches a climax preceding its extinction. The typical cursorial oreodonts pass into the *Eporeodon* stage. The hypertragulids are represented only by *Hypertragulus*.

Third and Final Phase, Promerycochœrus Zone

Upper John Day of Oregon. — Especially noteworthy in the Upper John Day is the sudden appearance of *Promerycochœrus*, an unheralded oreodont, which is highly characteristic of the close of the Oligocene and opening of the Miocene of North America. This Upper John Day level also contains members of the camel series (*Paratylopus*), animals of larger size, and similar to those in the Middle Oligocene. It is noteworthy that the only camels from the John Day obtained by the University of California expeditions come from this upper level.

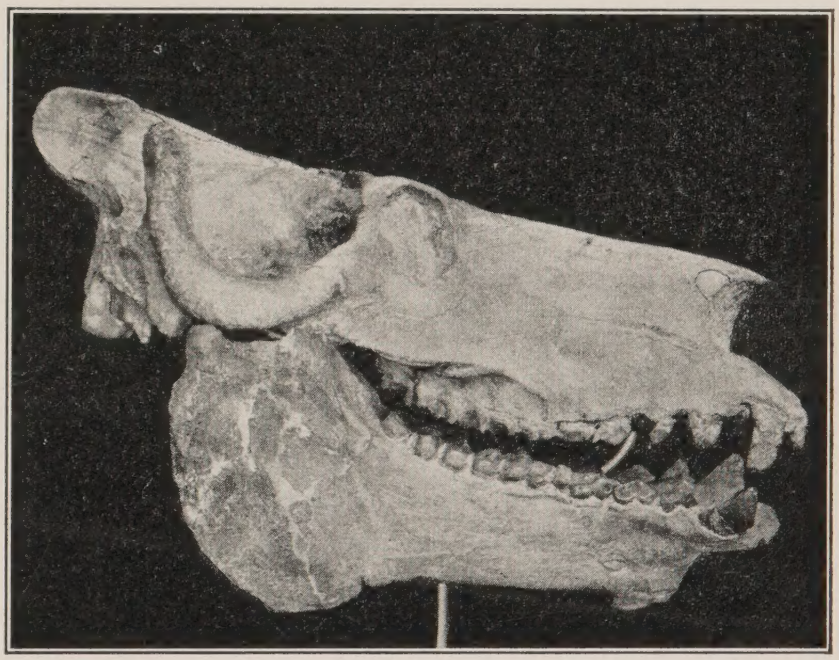


FIG. 115. — Type of the Promerycochœrus Zone. Skull of the Upper Oligocene oreodont *Promerycochœrus macrostegus*. In the American Museum of Natural History. After Matthew.

Great Plains of Dakota, the 'Harrison' and 'Rosebud.'—While the John Day Formation was gathering in Oregon, either a continuous but non-fossil-bearing deposition or a brief erosion interval followed on the Great Plains of Dakota, and the great formations variously known as 'Arikaree,' 'Gering,' 'Monroe Creek,' 'Harrison,' and 'Rosebud' began to be deposited conformably or unconformably on the summit of the White River group, or Leptauchenia Zone (Fig. 96). This great formation was recognized as Horizon D by Hayden as early as the year 1869. It is indicated by the horizontal lines in the map on p. 211, and is extensively exposed along the White, Niobrara, and North Platte rivers. It opens with partly flood plain or fine deposit conditions, interspersed with partly fluviatile or channel conditions, which are indicated by broad beds of conglomerates and river sandstones (Gering and Monroe Creek formations). The latter are non-continuous; they reach a maximum thickness of 200 feet, and are generally unfavorable for the preservation of mammalian life. The

conditions of deposition are more fully discussed under the Miocene, p. 278.

As soon as fossils become abundant it is evident that we are in the Promerycochœrus Zone, because, while the entire assemblage of mammals is, on the whole, similar generically to that of the Upper John Day, the specific stages are regarded as type for type more recent than those either of the Middle or even of the Upper John Day, or of the Aquitanian or St. Gérand-le-Puy of France. The peccaries afford similar testimony. *Thinohyus siouxensis* is more modified than any of the species of the John Day.[1] It is interesting to note that these peccaries, like those of the John

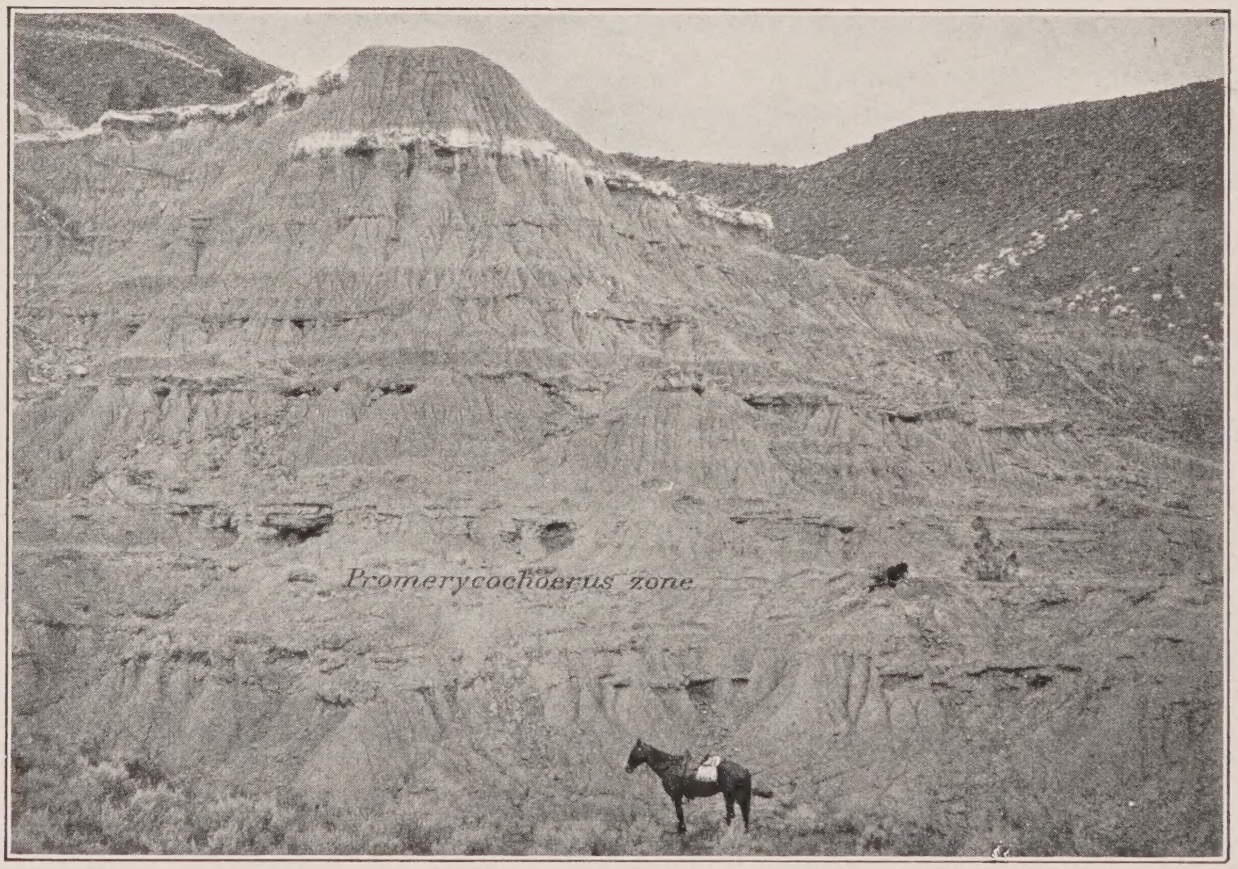
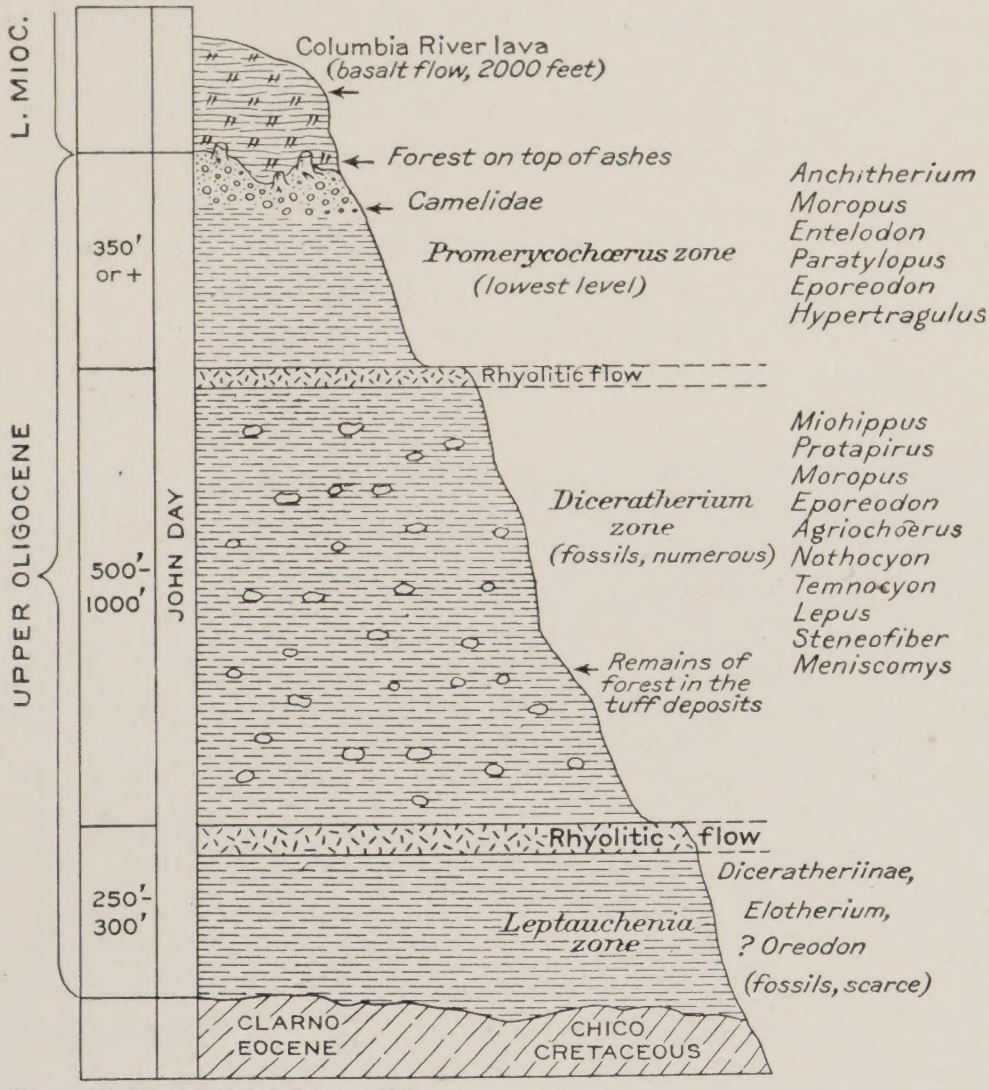


FIG. 116. — Upper John Day Formation, Oregon; Promerycochœrus Zone. Photograph by the University of California expedition of 1900.

Day, fall into two phyla, a dolichocephalic and a brachycephalic. This more recent character and the presence in these lower Arikaree deposits of the plains of several new genera of mammals may justify the placing of these formations in the Lower Miocene (Peterson, Matthew). We are certainly in the presence of a transition.

As compared with the Old World, however, it would appear that this mammalian assemblage of the Upper John Day, Lower Arikaree, Lower Harrison, and Lower Rosebud is still characteristically Oligocene rather than Miocene, as shown in the accompanying list.

[1] Peterson, O. A., New Suilline Remains from the Miocene of Nebraska. *Mem. Carnegie Mus.*, Pittsburg, Vol. II, no. 8, 1906, pp. 305–320.



By permission of the U.S. Geological Survey.

FIG. 117. — Section of the Upper Oligocene of the John Day, Oregon. After Merriam and Sinclair.

CHARACTERISTIC MAMMALS

Anchitheres (*Miohippus, Parahippus*)
Diceratheres (varied)
Tapirs
Chalicotheres (*Moropus*)
Entelodonts (last appearance)
Hypertragulids
(*Hypertragulus, Syndyoceras*)
Castorids (*Steneofiber*)
Camelids (varied)
Oreodonts
(*Promerycochœrus*)
Dicotylids (varied)
Leporids
Sciurids
Haplodontids

The older or surviving forms in this final Oligocene phase include advanced species of the oreodont *Leptauchenia*. *Steneofiber* is very abundant and characteristic; this is its last appearance. The final stages of *Aceratherium* and *Entelodon* (*Dinohyus*) are also observed here. Among the forms which are new or not previously observed are the anchithere *Parahippus*, a brachyodont, tridactyl horse which becomes very characteristic of the Miocene. Certain new and specialized oreodonts (*Mesoreodon, Phenacocœlus*) are found, besides the highly characteristic *Promerycochœrus* and the surviving *Leptauchenia*. It is

Characteristic Mammals
(*continued*)

Geomyids
Pro-Felids
Pro-Machærodonts
Canids (varied)
Mustelids

noteworthy that *Agriochœrus* is apparently extinct.

As we are now again observing the fauna of the Great Plains, it is not surprising to discover the excessively delicate and graceful cursorial camelid *Stenomylus gracilis*.

On the whole, however, browsing, slow-moving, river and forest-border and actual forest-living types prevail over open-plains and cursorial types,

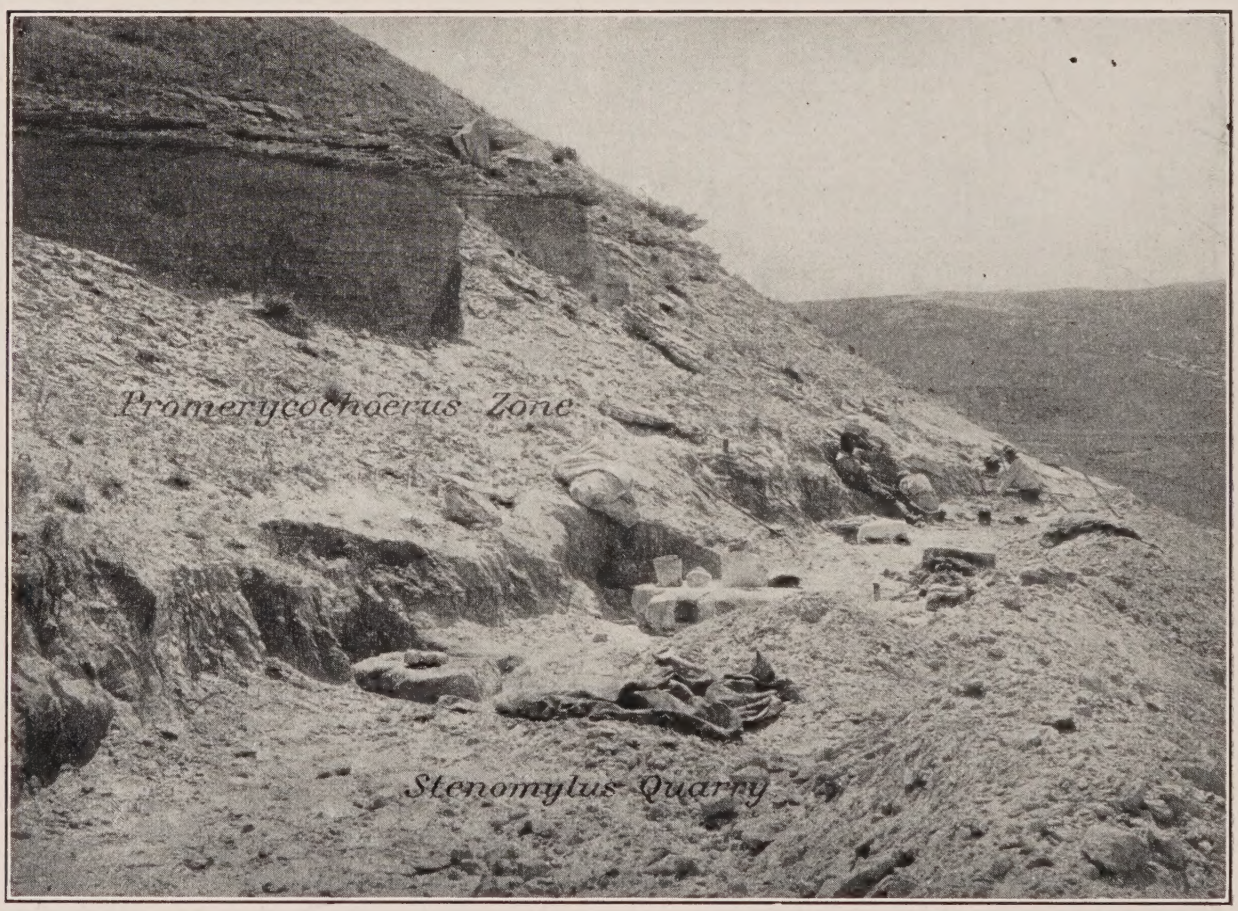


Fig. 118. — Summit of the Oligocene or Lower Miocene, Lower Harrison beds, Sioux County, Nebraska. A view of the *Stenomylus* quarry in the Promerycochœrus Zone. Photograph by American Museum of Natural History, 1908.

so far as we know the fauna of this region at this time. Undoubtedly an upland or plains and cursorial fauna existed in this western region, but it has not become fully known.

Physiographic conditions. — The geologic conditions of the Lower Arikaree, Lower Rosebud, and Lower Harrison are peculiarly interesting. Near the summit of the Lower Harrison occur the Dæmonelix beds of Barbour, named from the giant spirals or corkscrews of harder rock, which resist erosion, held together by fibrous material, and at many points stand out prominently against the sloping bluffs of the Upper Niobrara River. These were interpreted originally as representing the spiral roots of some

gigantic plant (Barbour, 1897 [1]); then as the burrows of the castorid rodent *Steneofiber*, remains of which were found to occur inside (Peterson, 1905) [2]; more recently Riggs [3] has reported skeletons of other animals drawn together within these spirals, a fact which tends to throw doubt upon the rodent 'burrow theory.'

Near the summit of the Lower Harrison stream bed formation is the extraordinarily rich deposit known as the Agate Spring Quarry, thoroughly

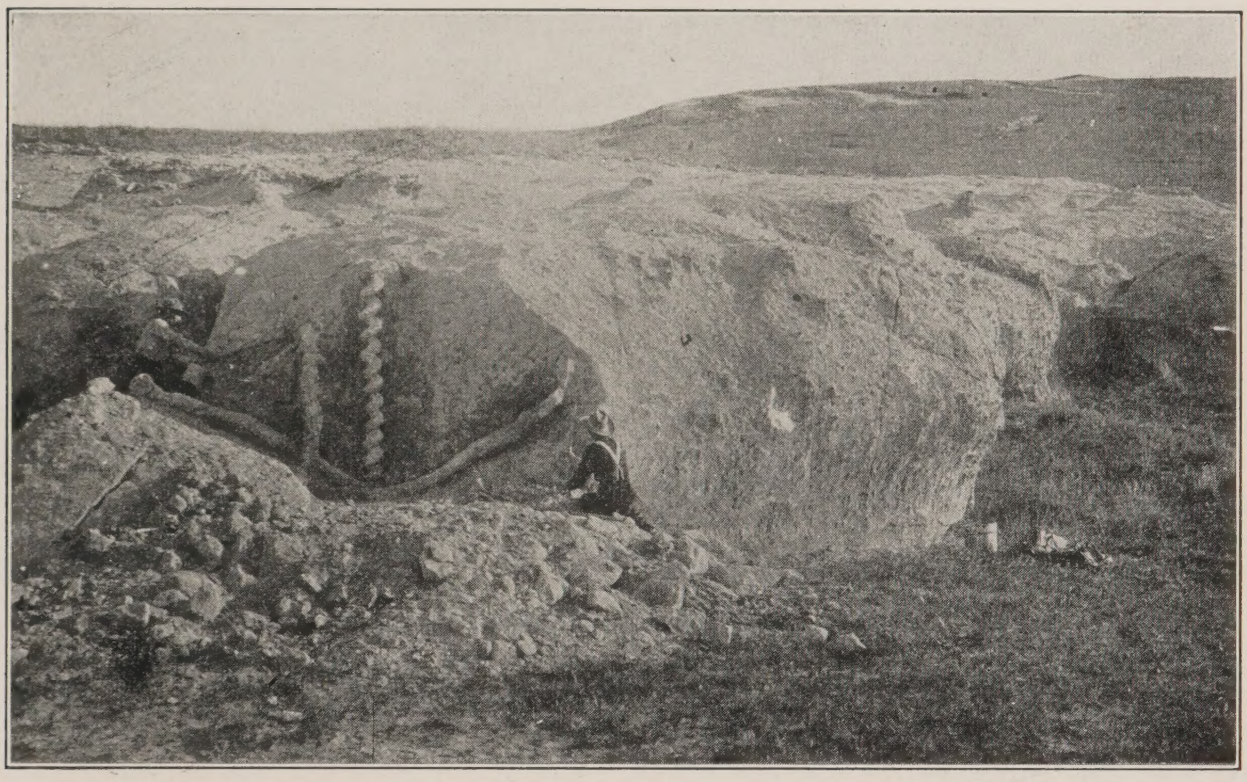


FIG. 119. — View of the Dæmonelix beds near Harrison, Sioux County, Nebraska, showing the problematical *Dæmonelix*, or "devil's corkscrews." From the Morrill Collection of Geological Photographs, University of Nebraska, by permission of E. H. Barbour.

explored by Barbour of the University of Nebraska and by Peterson for the Carnegie Museum, and yielding a nearly if not complete picture of the larger mammals of this region and period. Here has been found especially a complete skeleton of the giant chalicothere *Moropus* and of the giant entelodont *Dinohyus*, and smaller forms of *Diceratherium* in great abundance. This quarry was first reported by James H. Cook about 1890 in the center of a region rich in fossils.

The mammals of this period have been chiefly described by Barbour, Peterson (1906), and Matthew.[4] The last author, in describing (1907) the

[1] Barbour, E. H., On a New Order of Gigantic Fossils. *Nebr. Univ. Stud.*, Vol. I, no. 4, July, 1892; and Nature, Structure and Phylogeny of *Dæmonelix*. *Bull. Geol. Soc. Amer.*, Vol. VIII, April, 1897, pp. 305–314.

[2] Peterson, O. A., Description of New Rodents and Discussion of the Origin of *Dæmonelix*. *Carnegie Mus. Mem.*, Vol. II, 1905, pp. 139–191.

[3] Riggs, Remarks on *Dæmonelix*, *Amer. Soc. Vertebr. Pal.*, 7th. Ann. Meet., Baltimore, Dec., 1908.

[4] Principal titles are given in Bibliography.

Lower Rosebud beds, which lie farther east along the Pine Ridge of the White River, speaks of the entire fauna as an outgrowth of the Oligocene (White River and John Day faunas) containing no new or migrant elements.[1] Among the most peculiar forms are *Syndyoceras* (a collateral successor of *Protoceras* of the Leptauchenia Zone), a hypertragulid with an extraordinary development of the paired horns on top of the skull (Fig. 121), and *Stenomylus*, a small and delicately limbed cameloid abundantly found in one locality (Fig. 118). *Oxydactylus* (Fig. 144) is a long-necked, or giraffoid camel, the first of a very important Miocene and Pliocene series.

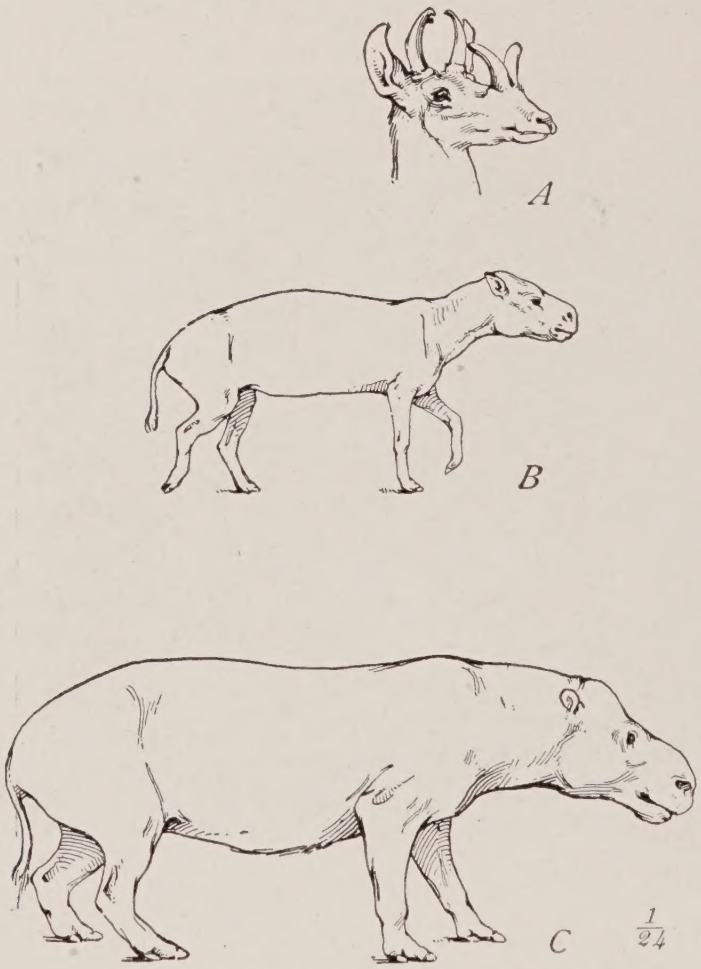


FIG. 120. — Contemporary Upper Oligocene or Lower Miocene mammals to same scale. By Charles R. Knight. *A. Syndyoceras*, successor to *Protoceras*. *B. Phenacocœlus*, successor to *Oreodon*. A browser or grazer. *C. Promerycochœrus*, precursor of *Merycochœrus*.

The hares, or leporids, are represented by species which cannot be separated from the modern genus *Lepus*, although the tooth pattern is primitive. The Equidæ are represented only by species with lateral toes, typically reaching the ground, with no vestige left of the pollex. The oreodonts are almost as abundant as in the Oreodon beds of the White River group. Especially remarkable is the group containing three specimens of *Promerycochœrus*, which is now mounted in the Carnegie Museum; the animals were huddled together as if overtaken by a sandstorm or sudden fall of volcanic ash. The canids range from the size of foxes (*Nothocyon*) up to the larger and more predaceous dogs (*Cynodesmus*), but include also the short-faced dogs (*Enhydrocyon*). A giant dog from the Lower Harrison was first defined as an amphicyon, but is now distinguished as *Daphœnodon* (Peterson). The peccaries, or dicotylids (*Desmathyus*), are still closely related to the *Perchœrus* type of the John Day. They are extremely abundant and characteristic in this zone.

In conclusion emphasis may be laid upon the fact that these plains formations are difficult to correlate in point of time, that they may be

[1] Matthew, W. D., A Lower Miocene Fauna from South Dakota. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIII, 1907.

By permission of E. H. Barbour.

FIG. 121. — Skull of the four-pronged ruminant *Syndyoceras*, found in the Dæmonelix beds of Sioux County, Nebraska. Univ. Nebr. Coll.

either: (1) Upper Oligocene, or (2) transitional from Oligocene to Miocene, or (3) of pure Lower Miocene age (see p. 277).

CAUSES OF EXTINCTION OF OLIGOCENE MAMMALS[1]

In considering Eocene extinction we have found (p. 172) the noteworthy feature in America to be the competition, or struggle for existence, between lower and higher types of mammals, or the archaic and modernized, as a result of which the former entirely disappeared.

In Europe this feature is less conspicuous than the apparent influence of the altered land areas of a peninsular region with the large number of consequent changes (p. 83). This is the more apparent in Europe because the archaic mammals do not appear ever to have had such a strong foothold in Eocene times as in continental America. We note the disappearance of a very large number of prophetic forms of modernized mammals

[1] Osborn, H. F., The Causes of Extinction of Mammalia. *Amer. Natural.*, Vol. XL, no. 479, Nov., 1906, pp. 769–795, no. 480, Nov., 1906, pp. 829–859.

such as palæotheres, lophiodonts, anoplotheres, xiphodonts, in part highly specialized and yet destined to extinction.

Doubtless the defective brain, the defective tooth, the defective foot contributed to the downfall of the prophetic modern types, and throughout Oligocene times we are able to concentrate our attention on certain specific organs, or parts of animals, as causes of extinction.

In general *those mammals appear to survive which present the highest adaptive combination of favorable characters in fully formed organs as well as the highest adaptability or capacity to further favorable change of habit or structure.* Conversely, inadaptive combinations of characters, such as of the brain, the limbs, the teeth, appear to have been the causes of extinction, partly in connection with changes of environment, partly because inherently or relatively inadaptive.

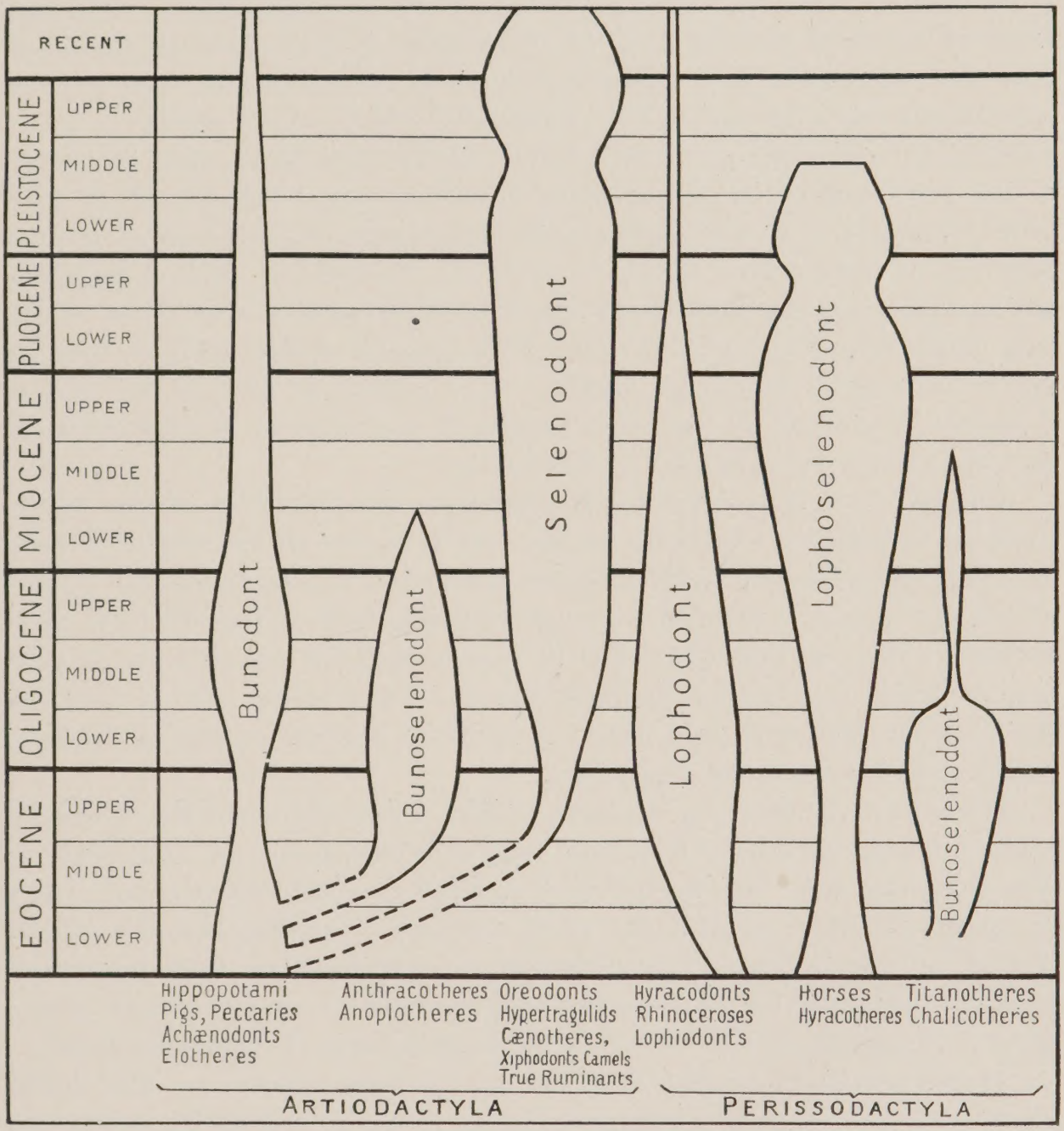
Thus in Oligocene still more clearly than in Eocene times we observe that extreme bulk, extreme specialization, and the development of certain dominant characters lead to extinction. Certain types of teeth or certain types of limb and foot structure simultaneously over large parts of the world have been found wanting and thus proved fatal to their possessors. These are the general lines of thought which have been followed by many authors since Darwin first directed our attention to this subject. It is desirable to look into some of these causes more critically.

Inadaptive foot structure. — As already remarked (p. 15), Kowalevsky observed in his great monograph (1873, p. 152), the extinction in Oligocene and Miocene times of all artiodactyls with inadaptive foot structure and inadaptive grinding teeth, as follows: Upper Eocene, *Xiphodon, Anoplotherium, Diplopus;* Oligocene, *Ancodus, Anthracotherium, Entelodon.* He pointed out that the inadaptation of the feet consisted in a mechanical defect in the small bones of the hand, or manus, while the inadaptation in the grinding teeth consisted in the persistent short, or brachyodont crowns composed of partially rounded cones and imperfectly formed crescents. By his theory the mechanically defective feet were incapable of acquiring the elongation into the cursorial type which saved the lives of the artiodactyls with adaptively formed front feet. The short-crowned teeth could not survive the change of vegetation from the softer herbage of Eocene times to the harder grasses of late Oligocene and Miocene times.

The accompanying diagram (Fig. 122) bears out Kowalevsky's generalization so far as the teeth are concerned. It exhibits the reduction in number of the mammals with short-crowned *bunodont* teeth toward the close of the Oligocene, and the reduction and extinction of mammals with *bunoselenodont* grinding teeth of two divisions, that is, both among the artiodactyl anthracotheres and anoplotheres and among the perissodactyl titanotheres and chalicotheres. The purely crested or lophodont types also appear to have suffered a reduction. The most highly successful dental types appear to have been the selenodont, characterizing all

the modern ruminants, and the lophoselenodont, characterizing the horses.

Titanothere grinding teeth. — We have seen the magnificent titanotheres suddenly cut off at the close of Lower Oligocene times, and this extinction may be attributed partly to the cone-and-crescent, or bunoselenodont



EVOLUTION OF UNGULATES IN NORTH AMERICA

FIG. 122. — The survival or extinction of mammals possessing certain types of molar teeth.

pattern of their grinding teeth, which were adapted to browsing on the coarse and soft rather than grazing upon the fine and hard kinds of food. Among these animals, nature was apparently making an effort to convert a brachyodont into a hypsodont crown by the elongation of the outer side of the superior grinding teeth; but this effort was futile because of the absence of a cross-crest and the persistent brachyodonty of the inner

side of the crown. Such a half-hypsodont, half-brachyodont tooth was not adaptive.

Some other cause, however, must be sought for the extinction of the titanotheres, because the entelodonts, with teeth still less effective mechanically, and the chalicotheres, with teeth very similar in pattern to those of the titanotheres, both survived through the Oligocene or even into Pliocene times in certain parts of the world. The obvious conclusion is that the entelodonts and chalicotheres either enjoyed some compensating adjustment or discovered a level habitat suitable to their needs.

Useless dominant organs.[1] — Another explanation which may be offered of the extinction of the titanotheres is that in two phyla the horns were over-developed, attaining gigantic size and causing an *incidence* of natural selection on characters which were useful in combat only. Characters which have reached an extreme stage so as to demand a larger share of the sum total of bodily nutrition than their general utility justifies may be known as useless dominant organs; they appear to violate the law of economy of growth, or the most favorable combination of characters by the subservience of each part to the whole.

But the force of this theory as applied to the extinction of the titanotheres is completely negatived by the fact that two of the phyla (*Titanotherium*, *Megacerops*) in which the horns were relatively small became extinct at exactly the same time as the large-horned genera (*Brontotherium*, *Symborodon*). We are thus compelled to believe that the titanotheres became extinct partly through the inadaptation of their *grinding tooth structure* to sustain their great bulk in a period of incipient desiccation and of changed conditions of climate and vegetation.

Diminution of browsing animals. — The Oligocene certainly witnessed a world-wide diminution of the larger types of browsing animals with brachyodont teeth and with feet incapable of rapid or cursorial locomotion. There is, on the contrary, an increase in the number of grazing animals, accompanied by an incipient transformation of brachyodont into hypsodont grinding teeth wherever the tooth pattern admits of such a change, and a general elongation of the feet from mesatipodal into dolichopodal types.

Multiplication of smaller browsing and grazing animals. — The multiplication of the small browsing and grazing animals, such as the oreodonts, in Oligocene times is also to be taken into consideration as a possible cause of extinction of the larger types like the titanotheres. The oreodonts certainly existed in enormous numbers, and must have consumed great quantities of food. The horses also swarmed in herds during the Oligocene periods in the region of South Dakota and Nebraska. It is possible that these animals may have cut off part of the food supply of the titanotheres. Their influence may be compared to that of the introduction of large numbers of sheep and goats into a cattle country. The abundance of new

[1] Cope, E. D., Primary Factors of Organic Evolution, 1896, p. 173.

forms of *dissimilar feeders* may disturb completely the balance of nature and alter the character and amount of food supply or even of the water supply in any given region.

The general conclusion as to Oligocene extinction is that climatic conditions, increasing aridity, development of grasses, incipient reduction of water courses, spread of meadow and savannah country, favored the evolution of Herbivora with long-crowned teeth and with elongate feet.

This period accordingly witnesses the first striking development of a tendency which becomes the dominant feature of Miocene and Pliocene evolution, namely, substitution of grazing cursorial types for browsing and ambulatory types, the latter being driven to the forests and water courses.

CHAPTER IV

THE MIOCENE OF EUROPE, ASIA, AND NORTH AMERICA

With the beginning of the Miocene we enter upon a new faunal phase in Europe. We also enjoy our first knowledge of the life of Asia. The hitherto pent-up mastodons of Africa enter Europe and later reach North America; Asia toward the close of the Miocene sends great contributions of its mammalian life into Europe and to a far less degree into North America. In all probability at this time Africa receives certain large contributions both from Europe and Asia, but of the exact period when this Eurasiatic contribution to Africa occurred we have no direct geologic record. The grand result of these intermigrations between the great continents is that by the close of the Miocene, Africa, Europe, and Asia probably constituted one zoölogical realm, ARCTOGÆA, with North America as an outlyer, distant but yet related.

This condition, which we shall speak of as the FIFTH FAUNAL PHASE, continues until the Lower or Middle Pliocene, when South America unites with North America and enters into this world-wide distribution of a somewhat similar fauna, namely, of proboscideans, horses, tapirs, true felids, and machærodonts, canids, mustelids, and many families of rodents.

V. FIFTH FAUNAL PHASE — MIOCENE TO LOWER PLIOCENE. APPEARANCE IN EUROPE AND NORTH AMERICA OF AFRICAN PROBOSCIDEA AND OF ASIATIC SHORT-LIMBED RHINOCEROSES. CLOSE UNION OF THE MAMMAL FAUNA OF EUROPE, ASIA, AND AFRICA. NORTH AMERICA MORE REMOTE, AND SOUTH AMERICA STILL ENTIRELY INDEPENDENT. PROGRESSIVE EXTINCTION OF BROWSING AND INCREASE OF GRAZING TYPES. A LOWERING OF TEMPERATURE. INCREASING SUMMER DRY PERIODS AND SEMI-ARID AREAS.

Palæogeography and Climate

Flora and climate of Europe. — There is evidence of a gradual lowering of temperature. While the vegetation of the Miocene has much in common with the Oligocene and is characterized by an increase of species, many forms now confined to warmer zones disappear from central and

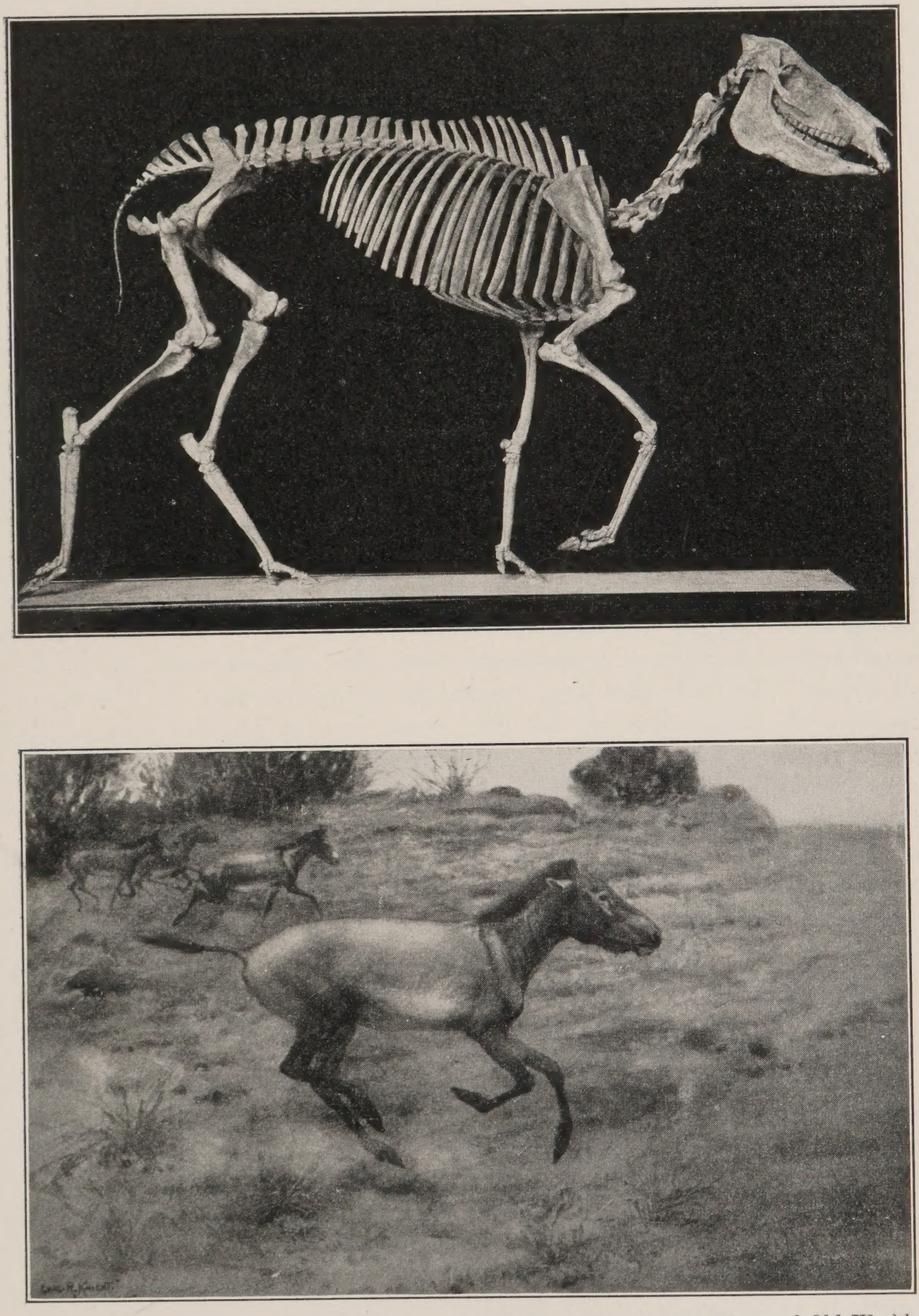


FIG. 123. — Type of the Upper Miocene 'Hipparion Fauna' of the New and Old Worlds. *Neohipparion*, the light-limbed desert-living horse of the Upper Miocene of North America. Above: Skeleton of *Neohipparion whitneyi*. Below: Restoration of the same by Charles R. Knight. Both in the American Museum of Natural History.

northern Europe. After the Lower Burdigalian, which is close to the Oligocene in character, palms cease north of the Alps, and toward the end of the Miocene there was a further fall in temperature, especially in the Arctic regions.[1] The absence of palms north of the Alps [2] is paralleled by their absence in the entire Rocky Mountain region of America from Colorado northwest. In consulting the earlier treatises of Saporta (1867) [3] and Heer (1865) [3] it is important for the student to note that at the time these works were written, the entire warmer Oligocene Period was embraced within the Miocene. We have few records of the development of grasses, but there is no question that Kowalevsky's generalization (1873), based upon the structure of the feet and teeth of mammals, that the Miocene was characterized by an increase of grassy plains, was correct; yet it is remarkable that only at the close of the Miocene of Europe do mammals with hypsodont, grazing teeth and stilted or cursorial limbs suddenly appear in large numbers; they are Oriental or exotic forms, which, however, were tempted to enter Europe by climatic and floral conditions to which they had become perfectly adapted in Asia and North America. If the palæontologist, observes Kowalevsky,[4] will imagine himself in the close of the Miocene, he will see great changes going on. Omnivorous forms are becoming graminivorous, the method of chewing is changing from a vertical, biting movement, to a horizontal, grinding one; and to meet these new conditions of feeding it is necessary that more durable teeth should be developed. The low teeth are replaced by columnar ones. It is in these anatomical changes that we find the surest proof of the existence of the great grassy plains and of the development of silicious plants. "However," observes Gaudry,[5] "grasses did not form a very large element of the vegetation even at this time." This was the beginning of the period of dry, grassy plains, similar to those of recent Africa, and extending through the greater part of the Pliocene.

Continental connections. — The emergence of the continents progressed in the Miocene. The great Mediterranean Sea of Europe and southern Asia was consequently reduced, and Africa, to the east at least, was united with Europe, permitting the northward migration of the mastodons and dinotheres. America was broadly united with eastern Asia, and the shutting off of the warmer southern currents from the polar region probably marked the commencement of a cooler northern climate. South America still remained separate; at least, there is no evidence of a faunal

[1] Schimper und Schenk, Palæophytologie, 1890, p. 820.

[2] Palms and camphor trees are recorded in the Middle Miocene beds of Œningen, 47° N. lat.

[3] See Bibliography.

[4] Kowalevsky, V., Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer natürlichen Classification der fossilen Hufthiere. *Palæontographica*, n.s., 2, 3, (XXII), 1873, p. 270 fol.

[5] Gaudry, A., Animaux Fossiles du Mont Léberon (Vaucluse). Étude sur les Vertébrés, p. 79. 4to, Paris, 1873.

interchange with North America. Australia also was separate. During this epoch or in the Pliocene may have occurred the union of the East Indies, Borneo, Sumatra, Java, with the Asiatic mainland, enabling the animals of Asia to populate these islands.

The coastal changes of southeastern North America resulted in the establishment of the main present outlines of the East Indies and Florida. Jamaica emerged after the close of the Oligocene; Cuba emerged after the

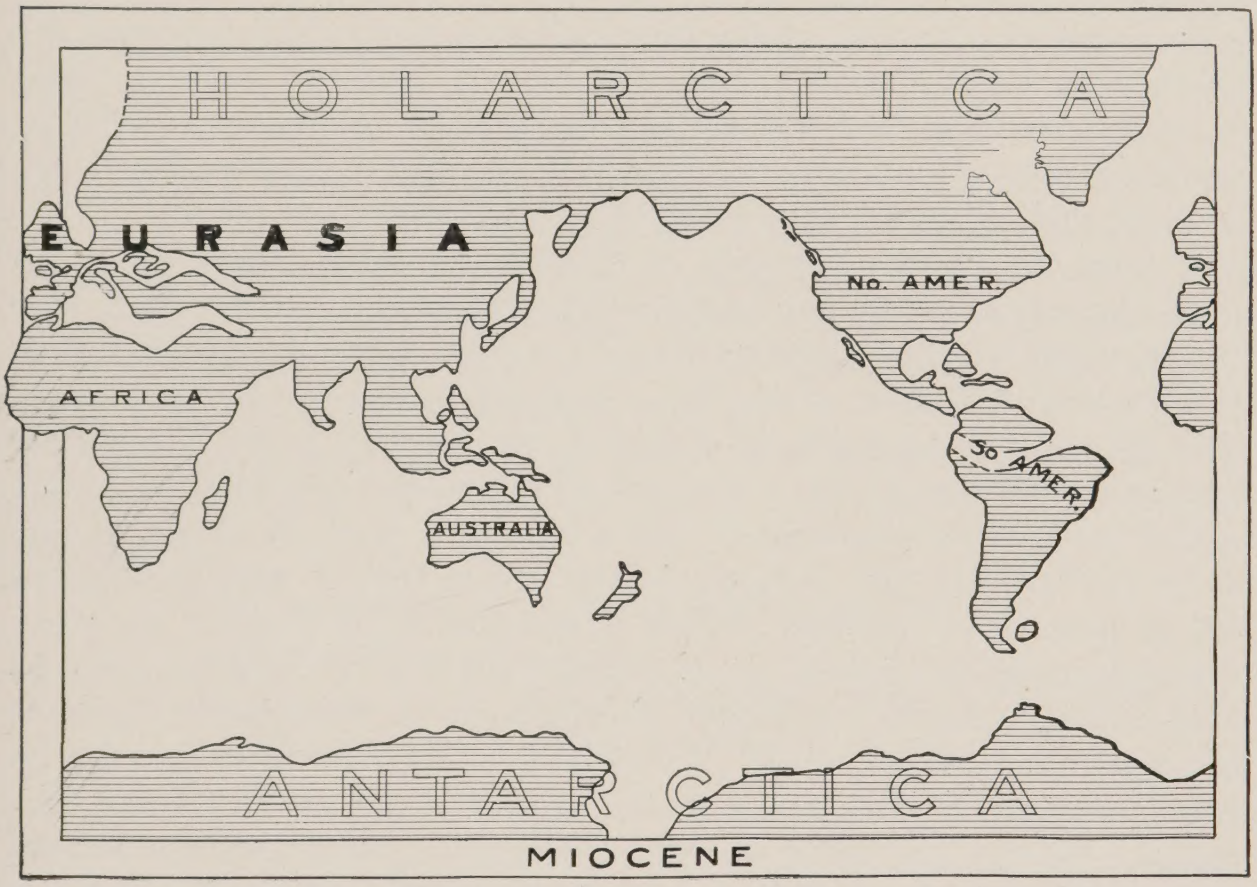


FIG. 124. — **Middle and Upper Miocene**, a period of continental elevation and emergence, consequently of renewed land connections and migrations. Africa broadly united with Europe across the Arabic peninsula, and a typical Asiatic fauna roaming westward into Europe and Africa. Asia connected with the East Indies and the Philippine Islands. Florida elevated at the close of the Miocene. South America divided into northern and southern halves by a broad gulf, the northern half perhaps connected with North America. Australia entirely separated from Asia. Rearranged after W. D. Matthew, 1908.

beginning of the Miocene; at the termination of the Miocene, Florida became a part of the continent; this continental connection of Florida is consistent with the appearance on this peninsula of an important part of the Upper Miocene fauna of North America in Lower Pliocene times.[1] Both Dall [2] and Hill [3] concur in believing that North and South America have been united from the Miocene to the present time.

[1] De Lapparent, A., Traité de Géologie, p. 1606.

[2] Dall, W. H., Geological Results of the Study of the Tertiary Fauna of Florida. *Trans. Wagner Inst.*, Vol. III, Pt. 6, 1903, pp. 1549–1550.

[3] Hill, R. T., Geological History of the Isthmus of Panama and Portions of Costa Rica. *Bull. Mus. Comp. Zoöl.*, Vol. XXVIII, June, 1898, p. 270.

Physiographic changes in Europe. — The Miocene witnessed the beginning of the phenomena which resulted in the formation of the great chain of Swiss Alps (Fig. 13, p. 59). At the very beginning of the period the lake basins of the Oligocene were gradually drained off and replaced by great river and flood plain deposits. Thus the initial or Burdigalian stage was just opening when the vast Lake of Beauce was drying up, leaving the *calcaires de Beauce* and *calcaires de Montabuzard,* the latter containing the earliest Miocene life.[1] Over this were poured the earliest sandy deposits (*sables de Chitenay*) of the great Miocene river which traversed the northern portion of France and emptied into the English Channel. These deposits of the *sables de l'Orléanais* are composed of formations of different stages, which together contain the typical Lower Miocene mammalian fauna. Thus the early Miocene life is recorded in 'continental formations.'

During the Middle Miocene, or Vindobonian stage, there was a renewed depression of the southern coast of Europe, while at the same time the lacustrine deposits of Sansan, Simorre, and St. Gaudens were laid down in southwestern France, giving us a complete record of Middle Miocene life. The coastal depression in the south was followed in the Upper Miocene, or Pontian Stage, by a renewed elevation and the fresh and widespread 'continental formations,' which give us a most wonderful picture of the life from the Isle of Samos in the east to that of western Spain, as well as of northern Germany. Thus at the close of the Miocene the south of Europe probably covered a tremendous land area favorable to and contemporaneous with the remarkable development of cursorial, herbivorous mammals, plains-living types, the climatic conditions being similar to those prevailing in East Africa at the present time.[2] Even at this time southern Europe was rather sharply distinguished from northern Europe in flora and fauna, probably on account of increasing desiccation. While at Pikermi (Greece) there were giraffes and antelopes, deer (forest types) were common north of the Alps.[3]

The enormous thickness of certain of the Miocene marine deposits (2,700 m.), and of the more massive freshwater deposits, together with these vast periods of elevation and depression, and the great changes in the mammalian life, combine to give us a realization of the great duration of Miocene time.

Miocene Life of Europe and America Compared

The Lower Miocene of Europe is very clearly defined by the sudden appearance of the proboscideans, including both mastodons and dinotheres.

[1] Mayet, L., Étude des Mammifères Miocènes des Sables de l'Orléanais et des Faluns de la Touraine. *Ann. Univ. Lyon,* n.s., I. Sci. Méd., fasc. 24, 1908.

[2] Depéret, C., Recherches sur la Succession des Faunes de Vertébrés Miocènes de la Vallée du Rhône. *Extr. Arch. Mus. Hist. Nat. Lyon,* 1, IV, Lyons, 1887, p. 249.

[3] Palacký, J., Die Verbreitung der Ungulaten. *Zoöl. Jahrb., Abt. Syst. Geog. Biol.,* J. W. Spengel in Giessen, Vol. XVIII, No. 2, 1903, p. 339.

In the coastal rivers there swarmed at this time sirenians (*Metaxytherium*), also originally from Africa. From Asia there appeared the first of the antelopes (*Protragocerus*). From Asia or from eastern Europe there appeared two entirely new phyla of rhinoceroses hitherto unrepresented in western Europe and unknown, namely, the excessively bulky and short-limbed teleocerine and the slender-limbed dicerorhine forms, the former destined to flourish and die out in Europe during the Miocene period, the latter destined to survive in the existing and rather primitive two-horned rhinoceros (*Dicerorhinus*) of Sumatra. In this phylum, to which we shall make frequent reference, the grinders are short, the horns are small and placed in tandem on the frontals and nasals. Probably from Asia also, there entered Europe the first of the higher primates, or anthropoid apes (*Pliopithecus*). From Asia also entered the first horned cervuline deer, or muntjacs. Of this Lower Miocene invading fauna the mastodons and teleocerine rhinoceroses alone reached North America. Distinctive also is the reappearance in Europe of horses in the *Anchitherium* stage either of north Asiatic or of North American origin.

The most characteristic of the larger forms of hoofed mammals which by the Middle Miocene become common to the New and Old Worlds are the following:

Primitive mastodons with four large tusks (new).
Chalicotheres, forest-living.
Teleocerine, or short-footed rhinoceroses, single-horned (new).
Aceratheres, large, hornless, tetradactyl rhinoceroses.
Tapirs.
Anchitheres.

Mingled with the new and strange invaders, some of the descendants of the great groups of Oligocene mammals continue their evolution both in Europe and North America, but certain of the most characteristic Oligocene types have passed their flourishing period and are in their last stages. These passing forms are the diceratheres, the anthracotheres, the enteledonts, which die out either at the close of the Oligocene or very early in the Miocene. Of all the mammals with bunoselenodont grinding teeth (see Fig. 122) the chalicotheres alone survive and are among the most highly distinctive forms of the Miocene.

FIG. 125. — Restoration of the head of *Dinotherium*, Miocene of Europe ($\times \frac{1}{36}$). After Gregory.

During the Lower and Middle Miocene the greater diversity of the American life as observed in the Oligocene continues. This is because we know the fauna of the drier regions in North America at this period, while

in western Europe we know only the mammals adapted to moister and better forested conditions.

In the Upper Miocene of Europe this contrast no longer obtains, for there is suddenly revealed a great fauna of dry plains and uplands; this fauna is similar to that of the drier parts of Africa and Asia of the present day, and to that of North America in Upper Miocene times.

Comparison between the Old and New Worlds in the Lower and Middle Miocene, or before this great upland element in Europe appears, is as follows:

Mammals of the Lower and Middle Miocene

Peculiar to Europe	*Common to Europe and North America*	*Peculiar to North America*
Dinotheres	Mastodons (trilophodont)	Camelids
Anthracotheres	Anchitheres	Protohippine horses
Tragulids (water chevrotains)	Tapirs	Antilocaprids, primitive
Horned cervuline deer	Rhinoceroses (aceratherine and teleocerine)	Oreodonts
True horned antelopes	Chalicotheres	Dicotylids, peccaries
Cricetines, or hamsters	Primitive hornless deer	Haplodontids, sewellels
Picas, or tailless hares	Mustelids	Geomyids, gophers
Leptictids or erinaceids	True felids	Heteromyids
Dicerorhine rhinoceroses	Machærodonts	Leporids, hares
Bears	Typical canids	?Cricetines
Viverrids	Canids (short faced)	Mylagaulids
True suillines	Amphicyonids	Procyonids
Sirenians (*Halitherium*, *Metaxytherium*)	Castorids, beavers	
	Talpids, moles	
	Murids, mice	

A very marked difference is seen in the prevalence of *Amphicyon* and the early appearance of the bears in Europe, and rarity of true canids of the wolf and fox type; while in America the canids abound and are widely varied, the bears are altogether absent and the amphicyons appear gradually.

America still has many of its own rodents, such as the sewellels (haplodontids), gophers (geomyids), and especially hares (leporids). The greatest diversity between Europe and America, however, is among the Artiodactyla; America is seen to be developing its own pigs or dicotylids, its highly diversified oreodonts and camels, its peculiar hypertragulids, including the ancestors of the American deer, and its own antelopes (antilocaprids), which are widely different from the true or bovine antelopes of Europe. The evolution of a distinctive plains fauna of North America is witnessed especially in the long-limbed and long-toothed varieties of the

horses, which rapidly evolve, as well as of the plains-living hares. Other contrasts will be brought out in detail as we follow the history of Europe and America independently.

The foregoing tables and contrasts show rather a unity of ancestral stocks than a genuine faunal reunion in the Lower and Middle Miocene of the New and Old Worlds, because the invasion of North America by the nomadic mastodons and teleocerine rhinoceroses cannot be cited as evidence of a widespread interchange of life. Thus we cannot draw close parallels between the Miocene divisions of the New and Old Worlds. They may be broadly divided as follows:

	Stage	*Fauna*	*Europe*	*North America*
Miocene	Upper, *Pontian*	Newer Miocene Fauna	of Pikermi and Eppelsheim	*'Loup Fork,' Hipparion Zone*
	Middle, *Vindobonian*	Older Miocene Fauna	of St. Gaudens, Simorre, and Sansan	*Deep River, Ticholeptus Zone*
	Lower, *Burdigalian*	Older Miocene Fauna	Sables de l'Orléanais, Brüttelen, and Eggenburg	*Arikaree, Merycochœrus Zone*

I. MIOCENE LIFE OF EUROPE

As indicated in our earlier discussion of this wonderful fauna (p. 246), the Miocene life of Europe may be divided into two grand phases, as follows:

The *Newer Fauna* of the Upper Miocene.	Second or Asiatic invasion, introduction of numerous plains-living, grazing, hypsodont types.
The *Older Fauna* of the Lower and Middle Miocene.	First or African invasion. Continuation and partial extinction of the Oligocene mammals. Continued prevalence of browsing, brachyodont, and river-border types.

The Older Fauna

Prevalence of browsing types. — In the *older fauna* we observe the dying out of all the large Oligocene mammals except the chalicotheres. Of the large mammals the imposing element is found in the newly arriving mastodons and dinotheres, which gradually evolve throughout the Oligocene. Attention should be called to the fact that these huge animals, as well as the flat-horned antelopes (*Protragocerus*), the tapirs, the anchitheres, the teleocerine rhinoceroses, the chalicotheres among the Herbivora, are all rather clumsy or slow-moving forms. The prevailing Carnivora (*Amphicyons* and *Dinocyons*), highly characteristic of the period, are also clumsy and slow-moving. The relatively small and light-limbed tragulids (*Dorcatherium*) and cervulines (*Dicrocerus*) are related to the forest- and swamp-

living types of to-day. In short, this older Miocene fauna is devoid of any plains-living elements or any distinctive upland types, and this is in widest contrast with the grazing and cursorial mammals of the newer or Upper Miocene fauna.

The *newer fauna* is not a development of the older; it is a distinct and very important invasion both from Asia and Africa.

Lower Miocene or Burdigalian

The Miocene is said to be introduced [1] in the *calcaire de Montabuzard*, which records the return of the horses (*Anchitherium*). The overlying *sables de l'Orléanais* are fluviatile sands, laid down in successive stages

Fig. 126. — **Lower Miocene.** Burdigalian. FRANCE. — Sables de **1** *Neuville-aux-Bois* (Loiret), fluviatile, sables de *Rebréchien*, **2** *Marigny*, **3** *Fay-aux-Loges*, **4** *Beaugency*, **5** *Tavers*, **6** *Les Barres*, *Artenay*, marnes du *Blésois*, calcaire de *Montabuzard* (Loiret), lacustrine. Sables de **7** *Chilleurs*, *Chevilly* (Loiret), **8** *Neuvilly*, near Belgian frontier, fluviatile. Sables de **9** *Ruan*, north central France. Calcaires et marnes de **10** *Suèvres* (Loire-et-Cher). Faluns et calcaires de **11** *Pontlevoy*, faluns et sables de *Thenay*, in la Touraine. Sables de **12** *Chitenay* (Loire-et-Cher), fluviatile. Faluns de **13** *Manthelan*, in la Touraine, marine. **14** *Saint-Nazaire-en-Royans* (Drôme). Mollasse blanche de **15** *Angles* (Gard). LOWER-AUSTRIA. — Mollasse of **16** *Eggenburg*, marine. Marine deposits of **17** *Linz*. SWITZERLAND. — Muschelsandstein von **18** *Brüttelen*, **19** *Macconens*, *La Molière*, **20** *Bucheggberg*, western Switzerland, marine. PORTUGAL. — Mollasse of **21** *Horta de Tripas*, near Lisbon. GERMANY. — Spalte der Schieferbrüche von **22** *Solenhofen* (Bavaria). Correlation of Depéret.

which contain the entire rich Lower Miocene fauna, parallel with which are widely scattered deposits in France, Germany, Austria, Switzerland,

[1] Mayet, Mammifères Miocènes des Sables de l'Orléanais, 1908, p. 314.

and far to the southwest in Portugal near Lisbon. In this Lower Burdigalian stage the flora of Auvergne (*Myrica, Cinnamomum, Liquidambar*) indicates a warm and dry climate.[1] In the strata of the basin of Mayence the Oligocene flora, *Sabal, Sequoia, Laurus, Cinnamomum,* also persists.[2] The marine cetacean of the period is *Squalodon bariensis.*

The Lower Miocene mammals are very widely distributed from India (Sind) on the east to Portugal on the west, and singularly uniform in species. Of the surviving Oligocene forms the robust anthracothere *Brachyodus* is especially widespread and characteristic of the Lower Miocene; it is the last survivor of this great Oligocene stock. Among perissodactyls, it is interesting to note the survival of the pair-horned rhinoceroses (*Diceratherium*), a line also about to disappear. Arising from Oligocene ancestors and highly characteristic of the entire Miocene period are the descendants of three other lines of perissodactyls, namely: the tapirs (*Paratapirus*), the aceratheres (*Aceratherium*) and the aberrant chalicotheres (*Macrotherium*).

The views of Stehlin are somewhat different from those of Mayet. He regards (1907) [3] the fauna of the *sables de l'Orléanais* as preceding that of Montabuzard and as composed of two elements of very different origin. One is indigenous to Europe and has survived from the Oligocene, the other is foreign, recently immigrated from an unknown center, probably from central Asia. Although we now know that the mastodons originated in Africa, the forms that accompanied them when they first appeared in Europe may lead one to suppose that they reached Europe by way of southern Asia. The forms that have developed directly out of the European Oligocene fauna include: *Amphicyon, Steneofiber, Palæochœrus, Hyotherium, Brachyodus.* Among the immigrants are: *Mastodon, Dinotherium, Anchitherium, Rhinoceros* [*Teleoceras*] of the *T. aurelianensis brachypus* type, *Listriodon, Chœrotherium, Hyœmoschus?, Palœomeryx* cf. *Kaupi.* The different deposits of the *sables de l'Orléanais* are not, as was formerly supposed, identical in age. To the differences in age as well as to the differences in location may be ascribed the fact that the various faunas are not exactly equivalent. The faunas of the successive stages of the *sables* are increasingly similar to that of Montabuzard, although none of them seem to be quite as modern; in other words, the *calcaire de Montabuzard* is held to be more recent than the *sables.*

The Lower Miocene horse *Anchitherium aurelianense,* described by Cuvier himself from the *sables de l'Orléanais,* is a small, relatively primitive, three-toed horse with brachyodont molars, in which the cones and conules are very distinct, teeth quite similar, in fact, to those of certain of the

[1] Boulay, 1899, and Giraud, *C. R.*, Vol. CXXXI, p. 916.

[2] De Lapparent, A., Traité de Géologie, 1906, p. 1604.

[3] Stehlin, H. G., Notices Paléomammalogiques sur quelques Dépôts Miocènes des Bassins de la Loire et de l'Allier. *Bull. Soc. Géol. France,* Ser. 4, Vol. VII, 1907, pp. 525–550, 536, 543.

North American Upper Oligocene anchitheres. Most surprising is the new, broad-headed rhinoceros (*T. aurelianensis*), named *Teleoceras* by Hatcher [1] from the presence of a horn at the very tip of its nasals, with a rudiment of a second horn in the center of the frontals, as observed by Gaudry. This animal is in all probability from northern Asia, and is destined to become

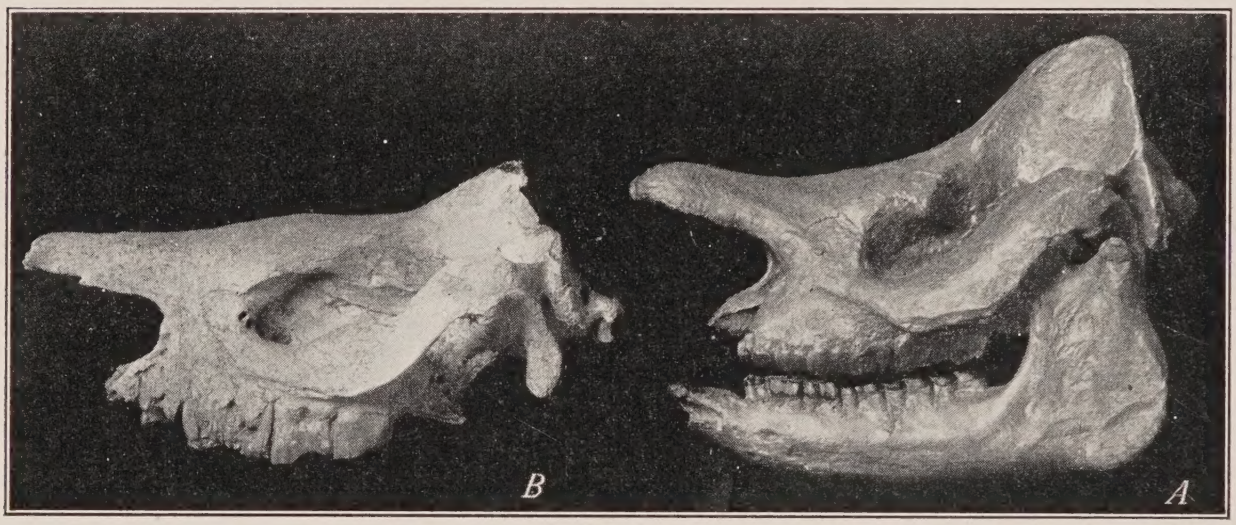


FIG. 127. — Skulls of the French and American teleocerine rhinoceroses. (*A*) *Teleoceras aurelianensis* (cast), (*B*) *Teleoceras medicornutus* (original). In the American Museum of Natural History.

one of the most distinctive and widespread of Miocene rhinoceroses; although short-footed, or brachypodal, and short-limbed, it was a great traveler; its range extended to Florida. The small narrow horn at the tip of the snout was probably an effective defensive weapon. The aceratheres, or hornless companions of *Teleoceras*, are distinguished by relatively slender limbs and tetradactyl fore feet; the nasals are narrow, pointed, and typically smooth, but they occasionally show the rudiments of a small horn. These animals are decidedly dolichocephalic. As above noted, in the Burdigalian beds of Portugal there occurs a third phylum of rhinoceroses, a diminutive form (*Dicerorhinus tagicus*) [2] distinguished by horns on both the nasals and frontals, and remotely ancestral to the existing rhinoceros of Sumatra.[3] We shall speak of these animals as Sumatran rhinoceroses or dicerorhines. A diminutive ancestor of the dicerorhine phylum has also been recently discovered in the *sables de l'Orléanais*, and Roman [4] believes that there existed in Europe two phyla of these dicerorhine rhinoceroses, one of more diminutive size, one of larger size, terminating respectively in the small and the large Upper Miocene races of *D. schleiermacheri*.

[1] Hatcher, J. B., *Amer. Natural.*, Vol. XXVIII, March, 1894, p. 241.

[2] Roman and Fliche, Le Néogène Continental dans la Basse Vallée du Tage (Rive Droite), 1ère Pt., Paléontologie. *Commis. Serv. Géol. Portugal*, Lisbon, 1907, p. 44.

[3] Thomas points out that the name *Ceratorhinus* Gray is preoccupied by *Dicerorhinus*.

[4] Roman, F., Sur un crane de Rhinocéros. *Soc. Linn. de Lyon*, Mar. 8, 1909.

CHARACTERISTIC LOWER MIOCENE MAMMALS

Anthropoid apes
(gibbons)
Mastodons
Dinotheres
Anchitheres
Tapirs
Rhinoceroses
Teleocerine
Dicerorhine
Aceratherine
?Diceratherine
Chalicotheres
Suillines
Horned cervulines
Tragulids, or chevrotains
Antelopes
(first Cavicornia)
Anthracotheres
(*Brachyodus* only)
Amphicyons
Dinocyons
Sirenians

Of the artiodactyls, beside the surviving anthracothere *Brachyodus*, we observe the pigs, recently monographed by Stehlin.[1] In the early Miocene he notes (p. 481) that the descendants of the Upper Oligocene *Palæochœrus* are becoming more sharply differentiated, the larger ones being gradually transformed into *Hyotherium sömmeringi* of the Miocene. There also appear two new invading forms (*Listriodon* and *Chœrotherium*), of remote relationship to the local suillines. Thus, like the rest of the mammals, the Suidæ are enriched by the arrival of new types at this time. "The faunal change," continues this writer (p. 482), "is perhaps the grandest that occurred in Europe during the entire Tertiary; no doubt it followed some far-reaching geological change; presumably communication was reëstablished with some great evolutionary center of the Old World."

The true selenodont artiodactyls are also reënforced by two fresh arrivals. Among the tragulids, a type closely related to the water chevrotains of western Africa (*Hyœmoschus*) now appears for the first time. The true modern tragulids (Tragulidæ) are a very primitive group of small ungulates, embracing two living genera, the Indian and Himalayan mouse-deer, or chevrotains (*Tragulus*), and the West African water-chevrotains (*Hyœmoschus*); *Tragulus* scarcely exceeds a rabbit in size; it suggests an agouti with unusually long legs, while the larger members of the family show some analogy to the musk deer.

Similarly the pro-Cervidæ are enriched by the appearance of horned cervulines (*Dicrocerus*), notable as the first horned artiodactyls to enter Europe, and closely similar to the existing muntjacs. A new cervuline, *Micromeryx*, also arrives, probably from Asia.

Marking a still wider break from the Oligocene selenodonts is the reported occurrence (Stehlin) of the first representative of the great family of Cavicornia, or hollow-horned ruminants, in the antilopine genus *Protragocerus*, a small animal with horns laterally flattened, as in the existing goats.

The giant invader of the period is the narrow-toothed mastodon (*Trilophodon angustidens*),[2] named specifically from its long, narrow upper

[1] Stehlin, H. G., Über die Geschichte des Suiden-Gebisses. *Abh. Schweiz. paläont. Ges.*, Vols. XXVI, XXVII, Zürich, 1899–1900, pp. 1–527.

[2] The type specimen of *T. angustidens* is from the Middle Miocene.

and lower molar teeth, which are quite similar in proportion to those of the Oligocene *Palæomastodon* of North Africa. This animal was termed *Trilophodon* by Falconer because there are three transverse rows of cusps on the intermediate [1] grinding teeth, while the last grinder has four transverse rows. It is further distinguished by a long, projecting snout armed with four straight and forwardly projecting tusks. While this is the most widely prevailing Lower Miocene species, another mastodon with broader teeth also occurs. These animals are related to the intermediate forms of primitive mastodons (*T. pygmæus*) found in the Burdigalian or Lower Miocene of Algeria (Depéret).

The dinotheres are characterized by the absence of upper tusks and by a pair of lower tusks projecting *downward* in the lower jaw.

Of the predaceous or carnivorous fauna, the giant amphicyonids (*Amphicyon*) are the dominant forms. The canids are less numerous and varied than in America; the last of the Oligocene genus *Cephalogale* appear. The Mustelidæ, or marten and weasel family, is represented by several land-living genera (*Stenogale, Palæogale, Stenoplesictis*) as well as by the river otters (*Lutrictis, Lutra*), the first species of the modern genus of otters. The felids are represented by numerous machærodonts, or saber-tooth cats, and by the aberrant *Pseudælurus*, regarded by von Zittel [2] as related to the Madagascan fossa (*Cryptoprocta*), but of the size of a small panther.

Of the microfauna we first observe among the castorids that the genus *Chalicomys* replaces the *Steneofiber* of the Oligocene. There are also hamsters (*Cricetodon*), picas or tailless hares (*Myolagus*), talpids (*Talpa*), and *Galerix*, referred to the tupaiids or tree shrews by Depéret, to the erinaceids or to the leptictids by Leche.

Not the least noteworthy is the first alleged appearance [3] in Europe of *Pliopithecus*, a representative of the anthropoid apes, related to the existing gibbons of Asia, and undoubtedly Asiatic in origin. Stehlin [4] regards the anthropoids as absent from this *sables* fauna. Summing up the new contributions to the life of western Europe, they appear to be as follows:

From Africa	*From Asia*	*From North America*
Mastodons	Tragulids, or chevrotains	Anchitheres
Dinotheres	Horned cervulines	
	Teleocerine rhinoceroses	
	Sumatran rhinoceroses	
	Anthropoid apes	
	Antilopines (doubtful)	

[1] That is, the fourth premolar and first and second molars.

[2] Von Zittel, K., Handbuch der Paläontologie, 1, IV, 1891–1893, p. 667.

[3] Mayet, Mammifères Miocènes des Sables de l'Orléanais, etc., 1908, p. 317.

[4] Stehlin, Notices Paléomammalogiques sur quelques Dépôts Miocènes. 1907.

As regards the home of the first hollow-horned ruminants, or Antilopinæ, there is no evidence in the known Oligocene of Africa indicating the existence of the ancestors of the true ruminants or selenodont artiodactyls of this type. The Lower Oligocene artiodactyls of Africa appear to be overflow or outlying forms of the suillines and anthracotheres. Nor do hollow-horned ruminants appear in North America until a late geologic period, the Lower Pliocene; it is consequently probable that the antelopes, together with the entire stock of Cavicornia, including the Bovinæ, or cattle, originated in Asia.

It is interesting to cast a glance at conditions in the Iberian peninsula, at the mouth of the Tagus.[1] There was an encroachment of the Atlantic Ocean on Portugal during and before the Early Miocene, due to sinking of the Tagus basin, accompanied by the formation of sea border deposits near Lisbon (Horta de Tripas) containing mammalian remains. Here is found the smallest Sumatran rhinoceros known (*Dicerorhinus tagicus*), a dwarf ancestor of the *D. sansaniensis* of the Middle Miocene. *Teleoceras*, *Brachyodus* and *Palæochærus* also occur here: the latter (*P. aurelianensis*) is a small pig, known to have inhabited central France at this time and to have survived into the later Miocene of Switzerland. The felid *Pseudælurus transitorius* is a medium-sized form transitional between the larger Oligocene ancestors and its later and still smaller Middle Miocene descendants.

On the seashores of upper and lower Austria we again discover remains of sirenians (*Halitherium christoli*).[2] Another marine deposit is that of the molasse of Brüttelen,[3] Switzerland, representing a coastal formation occupied by an arm of the sea, in which were deposited the remains of terrestrial and freshwater animals mingled with marine forms. Here also are found tapirs, diceratherine and aceratherine rhinoceroses, suillines, cervuline deer, and of especial interest are the remains of an antelope, probably allied to *Protragocerus*, a small, thickset animal with short, conical bony horns, which inhabited the Rhone valley in the Lower Miocene period. Here again occur remains of the primitive narrow-toothed mastodon (*T. angustidens*) and of the felid *Pseudælurus*.

Middle Miocene or Vindobonian

The Middle Miocene, or Vindobonian, is distinguished by a few new arrivals, chiefly from Asia and partly from Africa. These are as follows:

Ancestral bears, or Ursidæ, several branches from Eurasia.

Old World or catarrhine monekys (*Oreopithecus*), related to the baboons, from Eurasia.

[1] Roman and Fliche, Le Néogène Continental dans la Basse Vallée du Tage, 1907, pp. 44–76.

[2] Abel, O., Die Sirenen der Mediterranen Tertiärbildungen Österreichs. *Abh. K.K. Geol. Reichsanst.*, Vol. XIX, no. 2, Vienna, 1904 (p. 215).

[3] Studer, T., Die Säugetierreste aus den marinen Molasseablagerungen von Brüttelen. *Abh. schweiz. paläont. Ges.*, Vol. XXII, Zürich, 1896, pp. 3–34.

Anthropoid apes (*Dryopithecus*), related to the chimpanzees, from EURASIA.

Hystricomorph rodents (*Hystrix*), related to the porcupines, from AFRICA.

The mammals of the Vindobonian stage, as listed in Depéret's epoch-making work,[1] show a grand geographic extension from western Portugal to the northern shores of the Caspian Sea, recorded in no less than sixty-

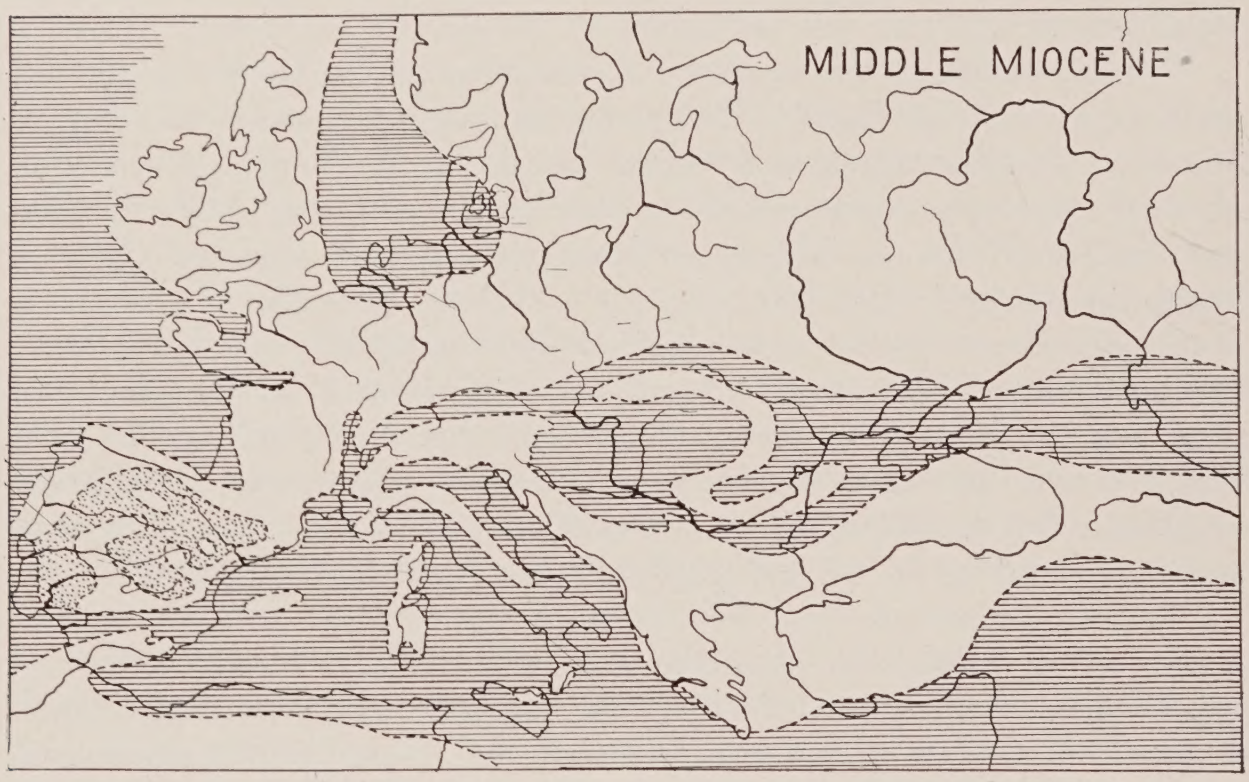


FIG. 128. — Europe in Middle Miocene or Vindobonian times. Dotted areas = lagoons. White = land. Ruled = sea. After de Lapparent, 1906.

eight fossil-bearing localities. The sirenian of the Middle Miocene is *Metaxytherium*.[2]

Physiography. — The Vindobonian, according to de Lapparent,[3] marks the beginning of the formation of the Alps and of the Himalayas; the Mediterranean Sea shrinks, and in its eastern part, which extended to the heart of Persia, is converted into land. The grand subdivisions of the Middle Miocene are those indicated by the coastal changes of southern Europe accompanied by successive and sharply defined deposition stages, with which the continental deposits of France, Austria, Switzerland, and Bavaria are broadly paralleled by Depéret as follows:

[1] Depéret, C., L'évolution des Mammifères tertiaires (Miocène). *C. R. Acad. Sci. Paris*, Vol. CXLIII, séa. Dec. 24, 1906, pp. 1121–1122.

[2] Abel, O., Die Sirenen der mediterranen Tertiärbildungen Österreichs, 1904, p. 215.

[3] De Lapparent, Traité de Géologie, 1906, p. 1606.

Marine Stages	*Continental Depositions*
Sarmatian	St. Gaudens, Œningen, Elgg, Käpffnach, Günsburg, Monte Bamboli, San Isidro.
Tortonian	Simorre, Steinheim, Grive-Saint-Alban, Mösskirch
Helvetian	Sansan, Eibiswald, Göriach, Georgensgmünd

The deposits are of the greatest variety, including the rich typical lacustrine deposits of Sansan and Simorre of southwestern France, formed in a large freshwater lake, as well as the lignites or swamp deposits of Styria (*Steiermark Braunkohle*), at Eibiswald, Wies, Göriach, and Voitsberg. These preserve Austria's contribution to the mammalian fauna. In Germany are the calcareous freshwater deposits of Georgensgmünd and Engelswies. Of the middle stage are the famous freshwater deposits of Steinheim and the fissure deposits of Mösskirch, which are parallel in age with the great fissure deposits of La Grive-Saint-Alban in France. Italy contributes to the upper stage the mammals of the lignites of Monte Bamboli. As observed by Osborn, and especially clearly defined by Depéret, there are three successive stages, typified by *Sansan*, *Simorre*, and *St. Gaudens*.

Stage of Sansan

The mammals of this oldest stage, discovered in 1834, described by Lartet[1] (1858) and more fully by Filhol[2] (1891), are contemporaneous with a rich bird fauna described by Milne Edwards[3] (1869–1871). The latter author observes that the bird fauna as a whole has no species in common with that of the Upper Oligocene of Allier; it is less abundant and less varied, and though it includes many water-loving birds, we find more non-aquatic forms mingled with them. It is certain that the African and Asiatic types are less numerous and that the temperate types are more numerous than during the Oligocene (p. 195). There are four birds of prey, namely: an eagle (*Aquila minuta*), of the size of the hen-harrier (*Circus cyaneus*); a sea eagle (*Haliætus piscator*), an undetermined species of eagle of large size, and an owl (*Strix*). Among passerines we know of a large, long-winged crow (*Corvus*), the remains of which are the most common avian bones found at Sansan; an aberrant passerine (*Homalopus*), presenting certain analogies to the hornbills, and thirteen small Fringillidæ, members of the family that includes the modern sparrows, finches, etc. There were two pheasants (*Phasianus*), one of which was larger than any recent pheasant, and three kinds of partridges (*Palæoperdix*), all extinct. About the waters of Sansan lived a heron (*Ardea*), slightly smaller than the com-

[1] Lartet, E., Notice sur la Colline de Sansan. *C. R. Acad. Sci. Paris*, Vol. 46, 1858.

[2] Filhol, H., Étude sur les Mammifères fossiles de Sansan. *Ann. Sc. Géol.*, Vol. XXI, 1, Art i. Paris, 1891.

[3] Milne Edwards, A., L'Histoire des Oiseaux Fossiles de la France, 1869–1871, Vol. II, pp. 579–582.

mon European heron, a small curlew (*Numenius*), and three ducks (*Anas*), one of which was very small and slender, one much like the recent duck

FIG. 129. — **Middle Miocene.** Vindobonian. Horizon of Sansan. FRANCE. — Calcaire de **1** *Sansan* (Gers), lacustrine. **2** *Jegun* (Gers). Faluns de **3** *Pontlevoy*, **4** *Sainte-Maure*, **5** *Manthelan*, in the basin of the Loire, marine. Mollasse de **6** *pont de l'Herbasse*, **7** *Bren*, **8** *Clérieux*, near Romans, marine. GERMANY. — Meeresmolasse (in Swabia) von **9** *Baltringen, Rammingen, Heggbach, Ursendorf, Hochgeland*, **10** *Hausen*, **11** *Niederstozingen*, **12** *Süssen.* Süsswasserkalk von **13** *Georgensgmünd*, **14** *Engelswies* (Bavaria). AUSTRIA-HUNGARY. — Braunkohle (in Styria) von **15** *Eibiswald, Wies*, **16** *Göriach, Gamlitz*, **17** *Voitsberg, Parschlug, Neufel, Leoben, Leiding, Feisternitz.* Marine sands of Grund at **17a** *Guntersdorf* (Lower Austria). Horizon of Simorre. FRANCE. — **2** *Bonnefond, St. Cristan* (Gers). **2a** *Villefranche d'Astarac*, calcaire de *Simorre* (Gers), lacustrine. Cinérites de **18** *Tournon*, in south central France. **19** *l'Isle-en-Dodon* (Gers). **20** *Saverdun* (Ariège). Mollasse de **21** *Mirabeau* (Vaucluse), marine. Marine deposits of **22** *Sorgues* (Vaucluse). Marine deposits of **23** *Romans* (Drôme). Sidérolithiques de **24** *La Grive-Saint-Alban* (in large part) (Isère), **25** *Mont Ceindre* (Rhône), **26** *Pretty near Tournus* (Saône-et-Loire), **27** *Gray* (Haute-Saône). GERMANY. — In Swabia, Bohnerz von **28** *Willmardingen, Jungnau* (in large part), Süsswasserkalk von *Steinheim, Ries, Urlau*, **29** *Nördlingen*, **30** *Althausen.* Bohnerz von **31** *Mösskirch*, **32** *Genkingen*, **33** *Heuberg*, **34** *Melchingen.* Gips von **35** *Hohenhöven* (Baden) (10 meters). AUSTRIA-HUNGARY. — In the intra-Alpine basin of Vienna, **36** *Dornbach, Vordersdorf, Loretto, Margarethen*, **37** *Fünfkirchen* (Hungary), calcaire de **38** *Bruck-a.-Leitha;* **39** *Breitenbrunn, Abstdorf-Franzensbad*, **40** *Mannersdorf*, **41** *Neudorf.* **42** *Trauenzinen* (Silesia). **43** *Krivadia* (Transylvania). **44** *Gyulu-Mendru* (Transylvania). **45** *Pesth* (Hungary). **46** *Ssoskut* (Hungary). RUSSIA. — **47** *Wosskressensk.* Horizon of Saint-Gaudens. FRANCE. — **48** *Valentine, Saint-Gaudens* (Haute-Garonne). **49** *Montréjau* (Haute-Garonne). SWITZERLAND. — Sands of **50** *Delsberg*, near Basel. **51** *Le Locle*, in the northwest. **52** *La Chaux-de Fonds*, in the northwest. **53** *Vermes*, near Basel. Mergelkalke von **54** *Œningen*, near Zürich, fresh water. Lignites of **55** *Elgg*, **56** *Käpffnach*, near Zürich. **57**, *Veltheim*, near Zürich, GERMANY. — In Bavaria : **11** *Günsburg, Reisensburg;* Sande von **58** *Häder, Dinkelscherben, Reichenau*, **59** *Diessen*, **60** *Dasing, Fraising, Tutzing, Stätzling, Reichertshofen*, **61** *Frontenhausen, Flinz of Munich.* **62** *Sankt Georgen* (Baden). AUSTRIA. — **36** *Heiligenstadt*, Tegel von *Hernals*, in Vienna basin. ITALY. — Lignites of **63** *Mt. Bamboli* (Tuscany). SPAIN. — **64** *San Isidro*, near Madrid. PORTUGAL. — **65** *Aveiras de Baixo*, near Oporto. RUSSIA. — **66** *Kriwoi-Rog* (Kherson). **67** *Nicolaieff*, at the mouth of the Dnieper. **68** *Sebastopol* (Crimea). **69** *Tiraspol*, near the mouth of the Dniester, Correlation of Depéret.

(*Anas*) in its proportions, and the third a very large, stoutly built form. There were also three different rails (*Rallus*), smaller than the Oligocene species found in the basin of the Allier, and including a land-rail and two marsh-loving forms or water-rails.

Around the lake borders [1] browsed the innumerable smaller ruminants, tragulines, and cervulines, the latter with forked horns (*Dicrocerus*) and present in great specific variety. Frequenting the marshes were three forms of pigs (*Hyotherium, Chœrotherium*), and the typical *Listriodon* with crested teeth like those of a tapir. Several species of flat-horned antelopes [2] are listed from this horizon. Of the perissodactyls the diceratheres have now disappeared; the anchitheres, tapirs, and rhinoceroses all present more advanced stages. Especially characteristic among the latter is the species *Dicerorhinus sansaniensis*, a delicate form which supports but two horns, a successor to the Lower Miocene *D. tagicus*. The chalicotheres are in the *Macrotherium* stage, a complete skeleton having been described from this level by Filhol, which enabled him for the first time to prove that the chalicotheres were not edentates, but of composite structure, with the teeth of perissodactyls and claws of digging type.

Fig. 130. — Clawed fourth digit of the foot ($\times\frac{1}{3}$) of the ancylopod perissodactyl *Macrotherium*, from the Middle Miocene of Sansan. After Gaudry.

The type of the great Miocene mastodon (*T. angustidens*) was discovered in this famous deposit. Bats, or Cheiroptera (*Vespertilio, Rhinolophus*) are numerous. Insectivores also abound, including several modern genera, hedgehogs (*Erinaceus*), shrews (*Sorex, Crocidura*), and desmans (*Myogale*); the latter are very similar to those now found in the Pyrenees and a few localities in Russia. Another insectivore, *Galerix* (syn. *Lantanotherium*) is, according to Leche, related to the Oriental erinaceid (*Gymnura*) now found in southeastern Asia and the East Indies. The rodents include squirrels (*Sciurus*), flying squirrels (*Sciuropterus*), dormice (*Myoxus*), picas (*Myolagus*), hamsters (*Cricetodon*), castorids (*Chalicomys*), and the peculiar family of theridomyids, soon to become extinct.

Preying upon this herbivorous fauna are the giant dogs *Amphicyon* and *Hemicyon*. Neither the true dog type (*Canis*) nor the cat type (*Felis*) has yet appeared. The leopard-like *Pseudælurus* represents the cats, while *Machærodus* represents the saber-tooth tigers. The mustelids were becoming more numerous, including martens, otters, weasels, while the Asiatic civets or viverrids (*Viverra*) are becoming somewhat more rare.

[1] Filhol, 1891, and Milne Edwards, 1869–1871, *op. cit.*

[2] *Protragocerus sansaniensis, P. martiniana, P. clavata.*

In the trees was found the gibbon-like ape *Pliopithecus*.

The chief mammalian faunas parallel with Sansan (Fig. 129, 1) are those of the freshwater calcareous deposits of Georgensgmünd (13) in Bavaria, and of the lignites of Eibiswald, Wies (15), Göriach (16), and Voitsberg (17) in Styria. Of the conditions in Styria, Hilber [1] states that in the early Miocene the sea advanced over parts of central and southern Styria, bringing in great southern molluscs with shells of wonderful hue. In the forests monkeys picked tropical fruits from the trees, and great powerful herbivores found abundant sustenance in the valleys, which were always free from snow. The carnivores hunted herds of muntjacs, such as are found in the East Indies to-day. These conditions are comparable with those now existing along the Bay of Tunis, but the temperature of the water of Tunis is not high enough to permit the growth of coral reefs such as flourished in the Miocene seas bordering Styria.

Stehlin [2] states that the known distribution of the Suidæ in the Middle Miocene is somewhat more extensive than in the Oligocene, *Hyotherium* and *Chœrotherium* extending into Austria, while remains of *Listriodon* have been found even in Asia Minor. During the transition from the Middle to the Upper Miocene (Stehlin, p. 483) the Suidæ become impoverished once more; the aberrant migrants (*Listriodon*, *Chœrotherium*) disappear, and only the central form *Hyotherium*, a survivor from the Oligocene ancestors, continues and undergoes further differentiation into the true pigs (*Sus*), which first appear in the upper stage. The same author (p. 475) believes that America received its Suidæ either from Asia or Europe in the Lower Oligocene or even earlier, the Eocene Chœromoridæ of France showing more points of affinity with the American Dicotylidæ (peccaries) than with any other forms.

Stage of Simorre and La Grive-Saint-Alban

This stage is characterized by an advance and by the introduction of a few new forms.

The lacustrine *calcaires de Simorre* (Fig. 129, 2*a*) directly overlie those of Sansan and are distinguished by mammals of more advanced specific stage. For example, the little two-horned Sumatran rhinoceros (*Dicerorhinus simmorrensis*) is more progressive than its ancestor *D. sansaniensis*.[3] Again, the *Pliopithecus* of La Grive, as described by Depéret, is a little nearer the gibbon (*Hylobates*) than that of Sansan. The best known mammals of this stage are those found in the fissure deposits, or *sidérolithiques*, of La Grive-Saint-Alban (24) (Isère), explored by Jourdan be-

[1] Hilber, V., Die sarmatischen Schichten vom Waldhof bei Wetzelsdorf, Graz SW. *Mitt. Naturwiss. Ver. Steiermark*, Jahr., 1896, No. 33, Graz, 1897, pp. 183–184.

[2] Stehlin, H. G., Über die Geschichte des Suiden-Gebisses, 1899–1900, p. 482.

[3] Osborn, H. F., Phylogeny of the Rhinoceroses of Europe. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIII, Art. xix. Dec. 11, 1900, pp. 258–259.

tween 1845 and 1861, and monographed by Depéret [1] (1887, 1892) and Gaillard [2] (1899). The latter author has increased the faunal list of La Grive to sixty-three species, and the new types he records all tend to emphasize the more recent age than Sansan of this remarkably rich fauna. The most famous parallel of La Grive is that of Steinheim (28), Württemberg, in which upward of thirty species have been recorded by Peters, Fraas,[3] and others, twenty of which are common with those of La Grive.

Of the physiography of this famous deposit of La Grive, Gaillard [2] remarks (1899, p. 77): "The fauna was so varied that from it we can deduce some ideas in regard to the region it inhabited. The presence of flying squirrels (*Sciuropterus*) and of certain tree-living forms of the insectivorous and carnivorous orders proves that the country was wooded; gentle streams flowed along the bases of the hills to collect in a lake or marsh at the bottom of the valley. The edges of this body of water were the haunt of rhinoceroses, otters, and of various birds. The numerous insectivores show that insects were abundant, and indicate a warm and humid climate. We are fully justified in assuming that the Dauphiné in the Miocene period had very much the general aspect of certain wooded regions in the tropics to-day." Depéret says (1887, p. 252) of this locality in the southeastern part of France that there was easy means of communication both with the Garonne valley and with Germany and Switzerland.

The chief and most interesting newcomer is the ancestral bear (*Ursavus primævus*), of which Schlosser [4] observes: "This is a small animal, showing certain resemblances to the short-snouted Malayan sun-bear (*Helarctos*), though not directly ancestral to it. It is in the main line of descent of the brown bear, being ancestral to the upper Miocene *Ursus böckhi*."

Gaillard sums up the fauna of La Grive (1899, pp. 75–78) as including one primate (*Pliopithecus*), seven bats, nine insectivores, sixteen genera, and many more species of carnivores, including the saber-tooth tiger *Machærodus jourdani*, a true feline (*Felis zitteli*) a little smaller than the domestic cat, three species of the feline *Pseudælurus*, the primitive bear (*Ursavus*), the large, extinct, bear-like dogs *Dinocyon* and *Amphicyon*, the otter (*Lutra*), three small mustelines of the genus *Mustela*, a number of civets (*Viverra* and *Herpestes*), and a genet (*Progenetta*). There are numerous rodents, among them squirrels, dormice, hamsters, picas. The probos-

[1] Depéret, C., Recherches sur la Succession des Faunes Vertébrés Miocènes de la Vallée du Rhône. *Extr. Arch. Mus. Hist. Nat. Lyon*, 1, IV, Lyons, 1887. Also, La Faune de Mammifères Miocènes de la Grive-Saint-Alban (Isère). *Arch. Mus. Hist. Nat. Lyon*, Vol. V, 1892, pp. 1–93.

[2] Gaillard, C., Mammifères Miocènes Nouveaux ou Peu Connus de la Grive-Saint-Alban (Isère). *Arch. Mus. Hist. Nat. Lyon*, Vol. VII, Lyons, 1899.

[3] Fraas, O., Die Fauna von Steinheim. *Jahreshefte Ver. vaterl. Naturkunde Württem.*, Vol. XXVI, Stuttgart, 1870. Also, Beiträge zur Fauna von Steinheim, *Jahreshefte Ver. Vaterl. Naturkunde Württem.*, Vol. XLI, Stuttgart, 1885.

[4] Schlosser, M., Über die Bären und Bärenähnlichen Formen des Europäischen Tertiärs. *Palæontographica*, Vol. XLVI, Stuttgart, 1899, p. 102.

cideans were represented by *Dinotherium* and *Trilophodon angustidens;* the perissodactyls by *Anchitherium* and two rhinoceroses, *D. simmorrensis* and *Teleoceras brachypus*, a successor of *T. aurelianensis* of the Lower Miocene. There was one ancylopod (*Macrotherium*), three pig-like forms (*Listriodon, Sus, Chœromorus*), among ruminants an antelope (*Protragocerus*), a chevrotain (*Dorcatherium*), and several cervulines, or deer-like forms (*Micromeryx*, and *Dicrocerus*).

A closely similar fauna existed on the plateaux of Bavaria and Swabia as described by Otto Roger.[1] He refers the bear of this region to *Pseudarctos*, one of the forms intermediate between the dog and bear families common in the Miocene. The remaining carnivores, insectivores, and rodents are closely similar to those of La Grive. Among the rodents are the flying-squirrels (*Sciuropterus*), now distributed in southern Asia and Holarctica. The proboscideans, perissodactyls, and suillines were also the same, the latter including the three Middle Miocene genera (*Chœrotherium, Hyotherium*, and *Listriodon*). The ruminants are abundant, varied, and exhibit great range in size. One of the larger animals is the brachyodont or browsing *Palæomeryx*, an Asiatic animal which also finds its way to America. It is of doubtful affinity. Of the three species of *Palæomeryx* recorded probably all were hornless, although attaining the size of existing deer or reindeer; they are to be regarded as precursors rather than ancestors of the deer. Schlosser has suggested their possible affinity to the family of giraffes. *Dicrocerus* is a cervuline of the size of the existing fallow deer, bearing forked antlers very much like those of the muntjac. These animals inhabited the woods of Bavaria in great herds. *Lagomeryx* is a tiny cervuline deer smaller than any living species. *Micromeryx* is a small, slender, long-legged ruminant, in Roger's opinion probably closer to the antelopes than to the deer. The flat-horned antelopes (*Protragocerus*) are represented by two species, and the water chevrotains by *Dorcatherium*, closely related to the recent hornless water chevrotain (*Hyœmoschus*) of Africa.

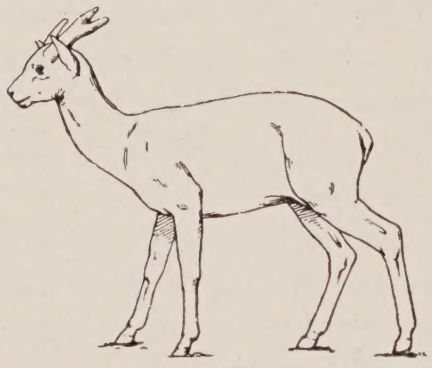


Fig. 131. — Middle Miocene *Dicrocerus* of Steinheim ($\times \frac{1}{24}$). After Fraas.

[1] Roger, O., Wirbelthierreste aus dem Dinotheriensande der bayerisch-schwäbischen Hochebene; and, Wirbelthierreste aus dem Obermiocän der bayerisch-schwäbischen Hochebene. *Ber. Naturwiss. Ver. Schwaben u. Neuburg in Augsburg*, nos. 33, 35, 36; 1898, 1902, 1904.

Stage of St. Gaudens, Œningen, Günsburg, and Monte Bamboli

MIDDLE MIOCENE MAMMALS

Gibbons
Baboons
Bear
Civets
Amphicyons
Canids
Porcupines
Flying squirrels
Tree shrews (very doubtful)
Mastodons (trilophodont)
Dinotheres
Tapirs
Anchitheres
Rhinoceroses (three phyla)
Chalicotheres
Antelopes
Cervulines (horned)
Chevrotains (hornless)
Palæomerycids (hornless)
Suillines (three phyla)

This concluding phase of the Middle Miocene is, according to Depéret,[1] typified by the fauna of St. Gaudens (Fig. 129, 48) on the head waters of the Garonne, which are paralleled (48–69) by the fresh-water deposits of Œningen (54), near Zürich, the lignites of Elgg (55) and Käpffnach (56); in the same region, the mammals of Günsburg (11) and Stätzling (60) in Bavaria, the lignitic fauna of Monte Bamboli (63) in Tuscany, and the deposits of San Isidro (64), near Madrid.

In the *Œningen beds* (which lie immediately above the strata of the Aquitanian Molasse in Switzerland, and are placed in the horizon of St. Gaudens, Middle Miocene, upper division, by Depéret) are many plant and animal remains. The flora,[2] consisting of nearly five hundred forms, is of a sub-tropical to temperate character, with, however, some tropical species. Palms are present, but very scarce. American types of trees are most frequent. Comparison should be made with the nearly contemporary forests of Oregon (Mascall) and of Colorado (Florissant), see p. 283. European trees stand next in number, followed in order of abundance by Asiatic, African, and Australian forms. Judging from the proportions of species found there, the total insect fauna may be presumed to have been richer in some respects than it now is in any part of Europe. The wood beetles were especially numerous and large. The waters were tenanted by numerous fishes, nearly all referable to living genera; also by crocodiles and chelonians.[3]

Middle Miocene primates. — It is remarkable that representatives of the Old World, or catarrhine monkeys, and of the anthropoid apes appear simultaneously in the Miocene of Europe, and are both represented by relatively large forms. Of these the cynomorph *Oreopithecus bamboli*, from the lignites of Monte Bamboli, Tuscany, is regarded by Gervais and Forsyth Major as standing nearer the anthropoids. It is true that the upper molars do resemble those of the anthropoid apes, while the lower molars resemble those of the baboons. The *Dryopithecus fontani* is unquestionably a true

[1] Depéret, L'évolution des Mammifères tertiaires (Miocène). *C. R. Acad. Sci. Paris*, Vol. CXLIII, Dec. 24, 1906, p. 1122.

[2] Heer, O., Flora tertiaria Helvetiæ, Winterthur, 1853–1859; also, Die Urwelt der Schweiz, 2d ed., Zürich, 1873.

[3] Geikie, A., Textbook of Geology, London, 1893 (p. 1001).

anthropoid; it is represented by three lower jaws and a humerus found in the Middle Miocene of St. Gaudens in southern France. From recent examination of all the discussions regarding this famous fossil, which has by some been placed near the line of human ancestry, Schwalbe [1] concludes that while the molars resemble those of man, this ape cannot be brought nearer, perhaps not so near, the line of human ancestry as the other anthropoids. How far *Dryopithecus* may be regarded as a stem form from which on the one side the line led to the human race and from the other to the living anthropoids, namely, the chimpanzee, orang, gibbon, and gorilla, cannot as yet be certainly determined. In one feature, the relative shortness of the humerus, this animal approaches the chimpanzee more closely than it does the other anthropoids.

Upper Miocene, Pontian

With this stage we enter the *newer Miocene fauna*, sometimes known as the *Hipparion* fauna, the most famous, the most widely distributed, and the best known of all the mammalian faunas of the Old World. It is highly distinctive and sharply demarcated from the older mammals by the new Asiatic, or Oriental, American, and possibly African mammals which it contains, especially by the great abundance of grazing and cursorial types which make their first appearance in southern Europe. These new forms are as follows:

Hipparions, fleet, grazing horses from Asia and North America.
Hares, or true leporids from Asia and North America.
Rhinoceroses, dicerine (genus *Diceros*), or atelodine (*i.e.* without cutting teeth), similar to those of modern Africa.
Giraffes, hornless, in great number and variety.
Antelopes related to the existing gazelles (*Gazella*), oryx (*Oryx*), elands (*Oreas*), harnessed antelopes (*Tragelaphus*), water bucks (*Cobus*), etc.
True deer, the roe deer (*Capreolus*).
Ancestral sheep (*Criotherium*).
Ancestral hyænas (*Ictitherium*).
Hyracoids or coneys (*Pliohyrax*), probably from Africa.
Aardvarks (*Orycteropus*) from Africa or Asia.

This new fauna, on the whole, is very distinctly similar to that of modern equatorial, east, or plateau Africa with the exception of the true Cervidæ, which never found their way into central Africa. However, it is rather Asiatic than African in origin and evolution; in short, many of these mammals appear to be on their way to Africa from Asia. Still another

[1] Schwalbe, G., Über fossile Primaten und ihre Bedeutung für die Vorgeschichte des Menschen. *Mitteil. Philomath. Ges. Elsass-Lothringen*, Vol. IV, no. 1, Decade 16 (1908), Strassburg, 1909, pp. 45–61.

view is that this fauna is an outlier of that which prevailed both in Asia and in Africa in Upper Miocene times. The various opinions on the important point of the origin of this Pontian fauna will be cited later.

With the advent of this new plains fauna, but especially with the advent of these new conditions of life in southern Europe, it is not surprising to find a temporary retreat of the forest fauna. The old Miocene browsing

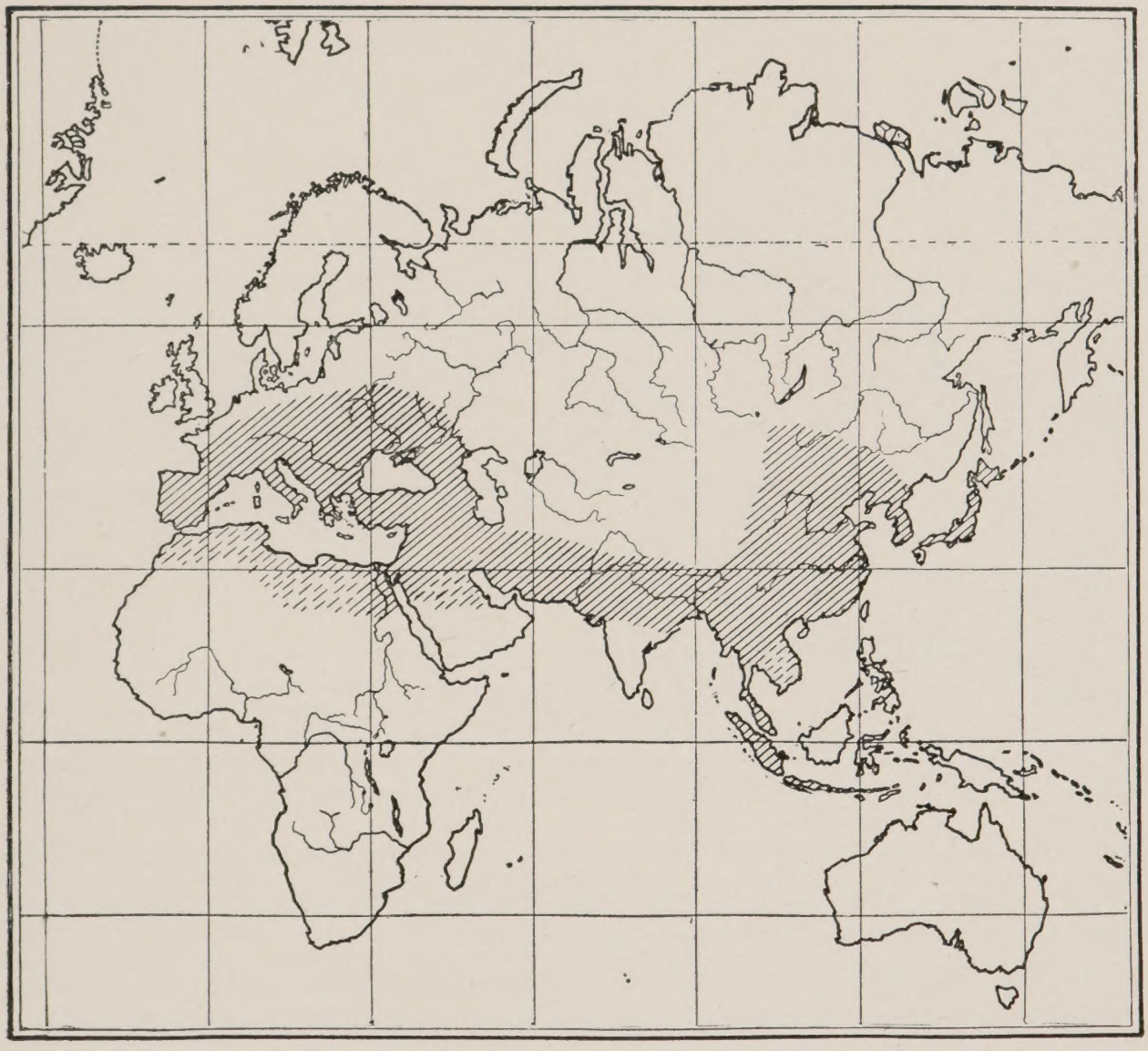


FIG. 132. — Distribution of the 'Hipparion Fauna' in the eastern hemisphere.

fauna is partly dying out, partly retreating to the north, partly returning to the forests, hillsides, and swamps of Asia and Africa.

Physiographic conditions. — De Lapparent[1] gives a clear account of the physiographic changes. In the Upper Miocene, or Pontian, the general recession of the sea, begun in the Middle Miocene or Vindobonian, continues until the Mediterranean Sea has almost wholly dried up, or become reduced to a number of brackish lakes. As a result Europe is broadly connected with Asia and Africa; the waters of the great basins of eastern Europe grow gradually less saline, and are replaced by the Caspian Sea

[1] De Lapparent, A., Traité de Géologie, 1906, p. 1622.

and other large sheets of increasingly fresh water, while brackish lagoons are formed between Sicily and the Rhone valley.

In the Congeria gravels of Austria, *Callitris* and the camphor trees (*Camphora*) as well as the acacias (*Acacia*) have vanished, but the sequoias (*Sequoia*) and the bamboos (*Bambusa*) continue. Beeches (*Fagus*) are much more abundant than in the preceding stages.[1] Greece at this period is covered with rich pastures inhabited by enormous herds of ruminants

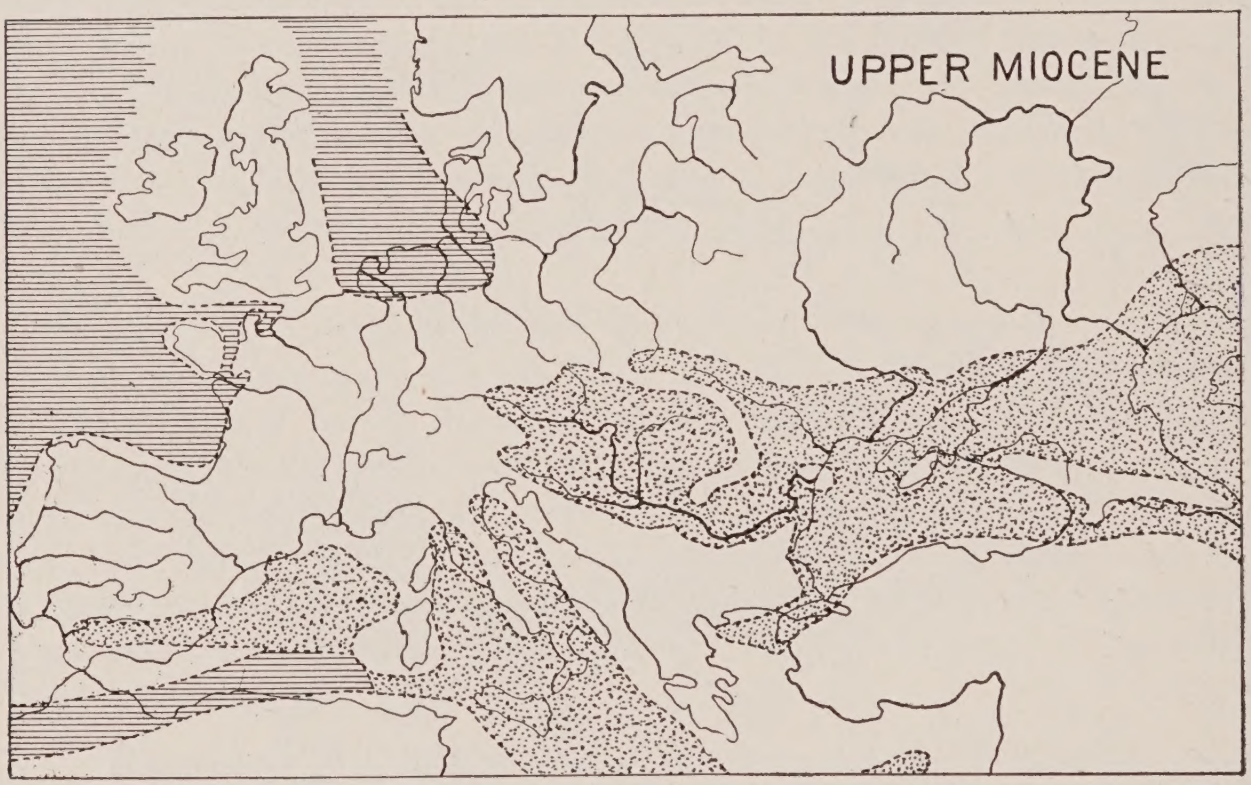


FIG. 133. — Europe in Upper Miocene or Sarmatian (Vindobonian-Pontian) times. White = land. Ruled = sea. Dotted areas = flood plains and lagoons. After de Lapparent, 1906.

and odd-toed ungulates. In no less than forty localities, extending from central Persia (Maragha) to western Portugal (Archino), the life of this great Upper Miocene stage has become known.

Typical deposits are those of the lake-bound Ægean region of Pikermi (Fig. 134, 1) giving us the typical southern fauna of the period, closely similar to that of the Isle of Samos (2) in the Ægean Sea, and Maragha. In Austria-Hungary are the beds of Baltavar (9). In Germany we get a glimpse of the more northerly mammals in the river gravels of Eppelsheim (40) near Darmstadt. The fauna of southwestern Europe is revealed in the deposits of Mont Léberon in Vaucluse (14), in the volcanic ash beds of Puy Courny (17) (Cantal), while further southwest are the deposits of Concud (31) in eastern Spain and Archino (32) in western Portugal.

It should be said that there is a difference of opinion as to the geologic epoch in which this fauna belongs, that the German geologist Lepsius[2]

[1] De Saporta, G., Le Monde des Plantes avant l'Apparition de l'Homme, Paris, 1879, p. 375.

[2] Lepsius, R., Geologie von Deutschland und den angrenzenden Gebieten, Pt. I, Stuttgart, 1887–1892, p. 637.

holds to the unquestionable Lower Pliocene age of Eppelsheim and consequently of Pikermi, of which Eppelsheim presents the northern facies, where the antelopes are replaced by deer. Depéret [1] and other writers of

FIG. 134. — **Upper Miocene.** Pontian. GREECE. — Red limonite of **1** *Pikermi.* ASIA MINOR. — **2** *Isle of Samos.* PERSIA. — **3** *Maragha* (omitted on map). RUSSIA. — **4** *Tchernigow*, in south central Russia. **5** *Sands of Balta*, in Podolia, southwestern Russia. Limestone of **6** *Odessa*, **7** *Groussolowo* (Kherson). ROUMANIA. — **8** *Manzati.* HUNGARY. — **9** *Baltavar.* Lignites of **10** *Baróth-Köpecz.* AUSTRIA. — **11** *Siebenhirten*, near Vienna. Congeria gravels of **12** *Vienna basin.* **13** *Eggenburg*, near Vienna. FRANCE. — Limons rouges de **14** *Mont Luberon* (Vaucluse). **15** *Visan* (Vaucluse). **16** *Aubignas* (Ardèche). Cinérites de **17** *Puy-Courny* (Cantal). Lignites de **18** *Saint-Jean-de-Bournay*, **19** *La Tour-du-Pin* (Isère). Marnes de **20** *La Trappe de Chambaran* (Isère). **21** *Mont Mirail* (Drôme). Lignites de **22** *Tersanne* (Vaucluse). Mollasse de **23** *La Croix-Rousse* (Ain), freshwater. **24** *Sainte-Foy-à Lyon*, near Lyons. Mollasse d' **25** *Ambérieu* (Ain), fresh water. **26** *Soblay* (Ain). **26a** *Saint-Jean-le-Vieux* (Ain). **27** *Rocher du Dragon*, near Aix (Bouches-du-Rhone). Marnes de **28** *Montredon* (Hérault). Lacustrine deposits of **29** *Estavar* (Cerdagne). **30** *Orignac* (Haute-Garonne) SPAIN. — Lacustrine deposits of **31** *Concud* (Arragon). PORTUGAL. — **32** *Archino*, on the Tagus. SICILY. — **33** *Grasitelli*, near Messina. GERMANY. — **34** *Salmendingen* (Bavaria). Bohnerz von **35** *Melchingen*, **36** *Trochtelfingen*, **37** *Ebingen*, in Swabia. **38** *Undingen* (Baden). **39** *Heuberg*, in Swabia. Kies von **40** *Eppelsheim*, near Worms (7–10 meters). Correlation of Depéret.

the French school are equally positive that this entire fauna should be regarded as Upper Miocene.

Pikermi. — Gaudry after his explorations between 1855 and 1860 gave a brilliant picture of the life of Greece in his great memoir of 1862.[2] He observed (p. 326 seq.) that vast plains probably extended eastward, connecting Greece with Asia, and beyond the arid Pentelicus and Hymettus

[1] Depéret, C., L'évolution des Mammifères tertiaires (Miocène), *C. R.*, 1906, p. 1123.

[2] Gaudry, A., Animaux Fossiles et Géologie de l'Attique, d'après les Recherches faites en 1855–1856 et en 1860 sous les auspices de l'Académie des Sciences, Paris, 1862.

there stretched verdant lowlands in which grassy plains alternated with magnificent forests. These regions harbored a varied mammalian life: here were two-horned rhinoceroses, huge bears, monkeys romping among the rocks, and carnivores, of the civet, marten, and cat families, lying in wait for their prey; grottos of Pentelican marble served hyænas as habitations, while immense troops of hipparions, like those of the quaggas and zebras in Africa to-day, occupied the plains. No less swift, and even more beautiful, were the antelopes, assembled in large herds according to their various species, and distinguished by the form of their horns. *Palæoreas* had spiral horns, *Antidorcas* lyre-shaped; in *Palæoryx* they were long and arched, in some species they resembled those of the gazelles, while *Tragocerus* had horns that approached those of the goats; *Palæotragus* was a slender, narrow-headed form with horns placed directly above the eyes. *Helladotherium* and a giraffe even more closely related to the recent ones were predominant in size among the ruminants. *Ancylotherium* was regarded (1862) as an edentate with hooked claws of huge proportions, but is now recognized as the last stage in the evolution of the perissodactyl chalicotheres. The most majestic animal of all was *Dinotherium*, which together with two kinds of mastodon represented the proboscideans. There was heard the roar of the terrible machærodonts, called saber-tooth tigers on account of their dagger-like upper canines. . . . There is a conspicuous absence of small animals (p. 333): beside some turtles, a lizard and some birds, there are only a rather large porcupine (*Hystrix*), a skunk-like form (*Promephitis*), and a marten (*Mustela*) slightly larger than the European marten of to-day. No trace of the bat nor of an insectivore has been discovered. The absence of small forms can be accounted for by the peculiar conditions of deposition of the Pikermi beds. The strong currents necessary to bring together the vast number of gigantic bones must have been sufficiently powerful to sweep all smaller ones away.[1] A. Smith Woodward believes that the Pikermi bone beds are due to some catastrophe by which the animals were suddenly destroyed at several distant points; the bodies were hurried by torrential floods through thickets or tree-obstructed water-courses before reaching the shallow basins in which they finally rested. This phenomenon appears to have been repeated. The hipparions, together with the numerous gazelles and probably *Helladotherium*, lived on the grass of the great prairies; certain giraffes were browsers, and *Palæotragus*, probably a long-necked form, but smaller than the giraffe, fed on the leaves of the lower branches of trees. The affinities of the Pikermi fauna, concluded Gaudry, are not with that of modern Europe, but of Africa, and this resemblance becomes more and more striking as we proceed to a closer examination of the faunas. We are thus led to the conclusion that at this time a land connection existed between Europe and Africa.

[1] Woodward, A. S., The Bone-Beds of Pikermi, Attica, and Similar Deposits in Eubœa. *Geol. Mag.*, n.s., Dec. IV, Vol. VIII, Nov., 1901, p. 485.

Characteristic life. — The mammals of southwestern France, of Mont Léberon, and Croix Rousse, were also described by Gaudry (1873),[1] and more recently by Depéret.[2] The smaller and more delicate build of the Rhone valley mammals as compared with those of Pikermi may be due, says Depéret (1887, p. 254), to the dry climate and scarcer nourishment which they met with, this being the northern limit of their distribution. Of artiodactyls, the suillines are represented by a giant species of true pig (*Sus major*), related to the living boars through the Pliocene forms. Of the surviving older ruminant fauna, *Palæomeryx* was a large and *Micromeryx* a small hornless deer, while the muntjac *Dicrocerus*, with its small bifurcated antlers, also was present. It is important to note that this is the last appearance of the horned cervuline deer in Europe. The roe deer (*Capreolus matheronis*) occurs here, although absent in the Pikermi fauna (Gaudry, 1873, p. 77). Side by side with the troops of gazelles (*Gazella deperdita*) with lyre-shaped horns, there existed *Tragocerus* with antilopine affinities but flattened horns that gave it a general goat-like appearance. The giant giraffe (*Helladotherium*), the most majestic of the ruminants of Europe, also occurs here. The rhinoceroses are of greater size, the Sumatran type *Dicerorhinus schleiermacheri* being provided with large horns; the hornless aceratheres also occur here (*A. incisivum*). Most striking is the fact that the brachyodont anchitheres have entirely disappeared, and that both the horses (hipparions) and antelopes are provided with long-crowned or hypsodont teeth. Among the carnivores, small and large, we still observe the plantigrade *Amphicyon* and the gigantic *Dinocyon*, also the primitive bear-like *Hyænarctos*, indicating an omnivorous radiation of this division of the Carnivora. Schlosser[3] (1899) observes that while *Hyænarctos* in a measure paralleled the bears in its evolution, it was not in the line of descent of *Ursus;* it possibly gave rise to the parti-colored bear (*Æluropus*) of Thibet. Notable among the rodents are two members of the true leporid family or hares (*Lagodus* and *Titanomys*), one of which is ancestral to the Corsican pica.

A very similar fauna has been more recently described[4] (Depéret, 1895) from Montredon (134) (Hérault), including evidence of troops of hipparions, antelopes, and gazelles. Especially notable here, as in Pikermi and Eppelsheim, is the absence of wolf or fox-like canids; this great family is represented only by the curious short-faced *Simocyon*.

To the north in Eppelsheim (Fig. 134, 40) the chief feature is the

[1] Gaudry, A., Animaux Fossiles du Mont Léberon (Vaucluse). Étude sur les Vertébrés. Paris, 1873.

[2] Depéret, C., Recherches sur la Succession des Faunes de Vertébrés Miocènes de la Vallée du Rhône. *Extr. Arch. Mus. Hist. Nat. Lyon*, 1, IV, Lyons, 1887.

[3] Schlosser, M., Über die Bären und Bärenähnlichen Formen des Europäischen Tertiärs. *Palæontographica*, Vol. XLVI, Stuttgart, 1899, p. 142.

[4] Depéret, C., Résultats des fouilles paléontologiques dans le Miocène supérieur de la colline de Montredon. *C. R. Acad. Sci. Paris*, Sept. 9, 1895.

greater abundance of deer, which replaced the antelopes of the south. The three older forms of rhinoceroses occur, successors of the Middle Miocene forms, such as *D. sansanensis*. The typical giant dinothere of Kaup (*D. giganteum*) occurs here.

To the east the mammals of Samos[1] and Maragha[2] are naturally close to those of Pikermi. In Samos occurs the hornless giraffine form *Samotherium*,

Fig. 135. — The Okapi (*Ocapia*), a primitive giraffe from the forests of the Congo. After Lankester.

very close to the existing *Ocapia* discovered in 1899 in the African forests. The aardvark (*Orycteropus gaudryi*) is found in both localities.[3] The range of all the characteristic antelopes of Pikermi to the far east in Persia is an evidence of their wide distribution in Asia. The Maragha fauna also includes a sivathere (*Urmiatherium*) which resembles that of the Siwaliks of India. In general the fauna of Maragha (see p. 332) closely approaches that of the Pliocene of southern Asia (Siwaliks) and of China (p. 332). To the far west a similar fauna (of Concud, Spain) has recently been described by A. Smith Woodward.[4]

[1] Forsyth Major, C. J., Sur un gisement d'ossements fossiles dans l'île de Samos, contemporains de l'age de Pikermi. *C. R. Acad. Sci. Paris*, 1887, p. 4; also Considérations nouvelles sur la faune des Vertébrés du Miocène supérieur dans l'île de Samos. *C. R. Acad. Sci. Paris*, Nov. 2, 1891.

[1] Schlosser, M., Die Fossilen Cavicornia von Samos. *Beitr. Pal. Geol. Österreich-Ungarns u. Orients*, Vol. XVII, Vienna and Leipzig, 1904.

[2] Kittl, E., Beiträge zur Kenntniss der fossilen Säugethiere von Maragha in Persien. I, Carnivoren. *Ann. K. K. Naturhist. Hofmus.*, Vol. II, Vienna, 1887.

[2] Rodler, A. und Weithofer, K. A., Die Wiederkäuer der Fauna von Maragha. *Kais. Akad. Wiss., Math.-Naturwiss. Cl.*, Vol. LVII, Vienna, 1890.

[3] Andrews, C. W., On a Skull of *Orycteropus Gaudryi* Forsyth Major from Samos. *Proc. Zoöl. Soc. London*, 1896, pp. 296–299.

[4] Woodward, A. S., The Lower Pliocene Bone-bed of Concud, Spain. *Geol. Mag.*, n.s. Dec. IV, Vol. X, May, 1903.

In all these localities the mastodons, as well as the dinotheres, now reached a higher phase of development. The mastodons are still 'longirostral,' or long-jawed, with large lower tusks. It is noteworthy also that while some of these mastodons (*T. pentelici*) are still in the trilophodont stage, *i.e.* with three ridges on the intermediate molars, the mastodon of Eppelsheim is a *Tetralophodon* (*T. longirostris* Kaup) with four ridges on the intermediate molars. Through the Pliocene of Europe and North America both kinds are found. The Pleistocene American mastodon is a descendant of a trilophodont phylum.

This fauna may be summarized as follows:

Mastodons
(trilophodont and tetralophodont, longirostral)
*Chalicotheres
(*Ancylotherium*)
Rhinoceroses
*Aceratheres
Sumatran types
*African types
*Teleocerines
Hipparions
Tapirs
Suillines
*Tragulids, or chevrotains
*Cervulines
True cervids or roe deer
First sheep, or ovids
Antelopes
*Giraffes
*Anthropoid apes
Catarrhine monkeys
Leporids (*Lepus*)
Castorids (*Castor*)
*Amphicyons
Felids
Hyraces, or coneys

The animals in the opposite column which make their last appearance in Europe at this time are indicated by a star (*). For several of these forms, such as the water chevrotains and the cervuline deer, this is not an extinction, but a migration. For other forms, such as the aceratherine and teleocerine rhinoceroses, this is apparently a period of extinction, although it is possible that *Aceratherium* survived in the north and gave rise to the giant *Elasmotherium* of the Pleistocene of northern Asia.[1]

Especially interesting is the arrival in Greece and Samos of the large hyracoid (*Pliohyrax*), undoubtedly of African origin. The hyraces, or dassies, are abundant and widely varied in the Lower Oligocene of Africa.

Upper Miocene primates. — Schwalbe[2] regards the Eppelsheim femur attributed to *Dryopithecus* as belonging rather to a true gibbon and thus deserving the designation *Pliohylobates eppelsheimensis* which has been given to it by Dubois. In the Upper Miocene appear two new and interesting forms, the first of which, *Pliopithecus antiquus*, is of a typical anthropomorphous type, spreading over all Europe, France, Switzerland,

[1] Osborn, H. F.: Frontal Horn on *Aceratherium incisivum*. Relation of the type to *Elasmotherium*. *Science*, n.s., Vol. IX, no. 214, Feb. 1899, pp. 161–162.

[2] Schwalbe, *op. cit.*, 1909, p. 55.

Styria, and Germany; it stands remarkably near the living gibbon, and is a smaller animal than either *Oreopithecus* or *Dryopithecus*. The other form from the Upper Miocene of Pikermi, *Mesopithecus*, is related in the abbreviation of its extremities, not to the tree-living, but to the true quadrupedal cynomorphs, or macaques; it is one of the earliest and most important representatives of this branch.

The Seven Rhinoceros Phyla of the Miocene

The polyphyletic law is in no group more brilliantly illustrated than among the rhinoceroses. The Miocene of Europe and North America opens with the discovery of two phyla, both descended from Oligocene ancestors, namely: (1) the pairhorned *Diceratheriinæ*, or diceratheres, (2) the hornless *Aceratheriinæ*, or aceratheres. To these are added in Miocene and Pliocene times four more great phyla, namely: (3) the *Teleocerinæ*, or teleocerine rhinoceroses, with a horn at the very tip of the nasal bones, with extremely short feet and limbs, hence also known as brachypodine. There also appear in the Lower Miocene the first of (4) the *Dicerorhinæ*, also known as the ceratorhine or Sumatran rhinoceroses, distinguished by two horns and large cutting teeth, and destined to play a very important part in Europe and survive in the existing Sumatran rhinoceroses; from these there branch off in late Tertiary and early Quaternary times the Etruscan and broad-nosed rhinoceroses, without cutting teeth. To these, at the summit of the Miocene and again in the Pleistocene, are added (5) the *Dicerinæ* or atelodine rhinoceroses, distinguished by two horns and the absence of cutting teeth (hence atelodine), surviving in the existing African rhinoceros. Then there appears, in the Pliocene of Asia only, the sixth great phylum of (6) *Rhinocerotinæ*, the typical or Asiatic rhinoceroses, with large, single, anterior horns and jaws armed with anterior cutting teeth; these survive in the existing Indian and Javan rhinoceros. A seventh phylum which may have branched off from the aceratherine branch is that of the (7) *Elasmotheriinæ*, giant hypsodont forms distinguished by a single posterior or median horn and known only in the Pleistocene of Europe and Asia. These phyla in several instances divide into sub-phyla; for example, the dicerorhine or Sumatran phylum, as noted above. The aceratherine phylum sends off branches in some of which the skulls acquire minute horns near the tips of the nasals. The dicerine, or African phylum, divides into long-headed forms, now typified by the 'white rhinoceros,' *D. simus*, and mesaticephalic forms, typified by the 'black rhinoceros,' *D. bicornis*.

1. Diceratheriinæ, the diceratheres.
2. Aceratheriinæ, the aceratheres.
3. Teleocerinæ, the teleocerines or short-footed rhinoceroses.
4. Dicerorhinæ, the dicerorhine or Sumatran two-horned rhinoceroses.

5. Dicerinæ, the atelodine or African rhinoceroses, two-horned.
6. Rhinocerotinæ, the typical or Indian rhinoceroses, single-horned.
7. Elasmotheriinæ, the elasmotheres (a possible side branch of II).

II. MIDDLE MIOCENE LIFE OF ASIA

The wonderful mammalian fauna of Asia still awaits stratigraphic arrangement; that is, the geologic or time succession of the mammals is still to be worked out. On this and on further exploration, especially of the smaller forms of life, depends the question of the origin and history of some of the most important Old World types. The earliest known mammals at present discovered in Asia are of Miocene age, and partly of Oligocene character compared with those of Europe, while the more recent are of Pliocene and Pleistocene age.

In India the main geologic distribution of the mammal beds, according to Oldham,[1] Blanford,[2] and Geikie,[3] is as follows:

II. Siwalik Group, newer, or chiefly Pliocene.
I. Manchhar Group, Sind, older, or chiefly Miocene.

The most striking feature of the *Lower Manchhar* mammals is their correspondence with those of the 'older Miocene' of western Europe, and the most mysterious feature is the absence in this fauna of ancestors either of the Upper Miocene life of Europe or of the Upper Miocene and Pliocene life of Asia; that is, western India at this time does not furnish us, as we should have anticipated, with the ancestry of the wonderful Upper Miocene and Pliocene fauna, but only with a very limited portion of this ancestry. This may be explained by the fact that this is chiefly a *forest or browsing* fauna.

Manchhar group. — In Sind (Fig. 136), resting on the marine Gáj of undoubted Lower Miocene age, on the flanks of the Kirthar Range, is the Manchhar series, 10,000 feet in thickness, composed of fluviatile, or flood-plain clays, sandstones, and conglomerates. Of these the Lower Manchhar beds are composed of ossiferous conglomerates, including bones and single teeth, the specific determination of which is often unsatisfactory. The Upper Manchhars are unfossiliferous. Since the Gáj beds are Lower Miocene, the Lower Manchhars cannot be older than Middle Miocene. This intermediate position is confirmed by the fact that they do not contain any typical Upper Miocene mammals, with the possible exception of two species. The *Bugti beds* in the southern portion of the Suleiman Range, consisting also of clays and sandstones interstratified with conglomerates 5,000 feet in thickness, have yielded near Dera Bugti a similar fauna.

[1] Oldham, R. D., A Manual of the Geology of India. 8vo, Calcutta, 1893.

[2] Blanford, W. T., Homotaxis, as Illustrated from Indian Formations. *Rec. Geol. Surv. India*, Vol. XVIII, Pt. 1, 1885, p. 37.

[3] Geikie, A., Text-book of Geology, 1893, pp. 1021, 1022.

It is apparent, first, that there is every reason why the term 'Siwalik' should not be applied to the Manchhar Zone; second, it is of interest to note that these Manchhar and Bugti deposits are apparently of river and

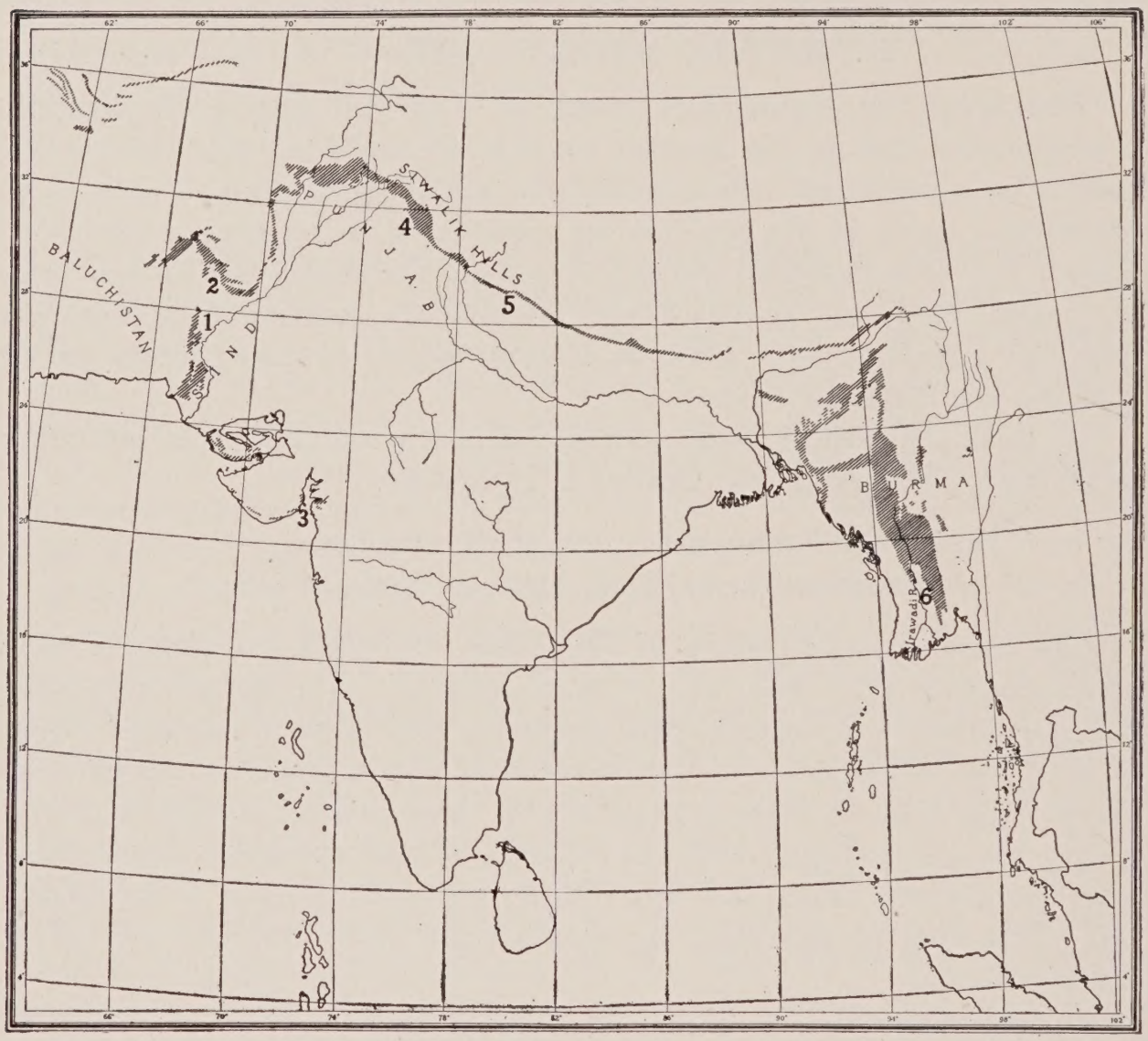


FIG. 136. — Map of India showing Tertiary formations containing fossil mammals (oblique lines). **1**. Manchhar Beds; **2**. Bugti Hills; **3**. Perim Island; **4**. Punjab Siwaliks; **5**. Subhimalayan Siwaliks; **6**. Beds of the Lower Irawadi. Modified from Oldham.

flood-plain origin, like the great American deposits which we have been considering.

Middle Miocene Life of India

These older mammals of western India (Manchhar and Bugti) are spoken of by Schlosser[1] as the 'Anthracotherium fauna' because of the presence of very large numbers of anthracotheres, large and small, including, beside *Brachyodus*, an animal we have seen to be very typical of the Lower Miocene of Europe, other species referred to *Hyopotamus* and *Anthracotherium*, and other mammals regarded as related to the anthracotheres, namely, *Hemimeryx* and *Sivameryx*. From the Bugti Hills, Pilgrim described in

[1] Schlosser, M., Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. *Abh. k. bayer. Akad. Wiss.*, Cl. II, Vol. XXII, Pt. 1, Munich, 1903.

1907 the giant anthracothere, *A. bugtiense*, and from the same horizon the tetraconodont anthracothere to which he gave the name *Telmatodon*.[1] The *A. bugtiense* is a brachyodont form closely resembling *Brachyodus*.

This fauna is sharply distinguished from the 'newer Miocene' fauna of Europe, as well as from the true Siwalik fauna of India, by the absence of *Hipparion*, as well as of all the other characteristic Upper Miocene types of Europe and Pliocene types of Asia. We should expect to find here large numbers of the ruminants, ancestors of the antelopes and of the cattle, but such is not the case. We do find, however, certain other Upper Miocene mammals in this fauna, indicating that it partly extended into Upper Miocene times.

The pigs are represented by animals referred to *Hyotherium*, a typical Miocene genus, and to *Sus* (*S. hysudricus*), a genus which, it will be recalled, first appears in the Upper Miocene of Europe. In this connection it may be noted that the specific and generic determinations of these animals probably require revision, since the determinations are old and many of them are based on imperfect types.

Beside the largely prevailing anthracotheres, the artiodactyls are represented by the water chevrotains (*Dorcatherium*), but not by any of the cavicorn or hollow-horned ruminants.

Especially interesting among the perissodactyls is the presence of a true single-horned Asiatic rhinoceros (*R sivalensis*), an animal not represented in Europe, but believed (Lydekker) to be an ancestor of the existing brachyodont or browsing type, the Javan[2] rhinoceros (*R. sondaicus*). Another species (? *T. perimensis*) is regarded by some writers (Lydekker) as a teleocerine rhinoceros, or as belonging to the genus *Teleoceras*. The hornless rhinoceroses, or aceratheres, are also numerous, being represented by the widely distributed Miocene species *A. b anfordi*.

That this is a browsing rather than a grazing fauna is still further emphasized by the absence both of horses and hipparions as well as of grazing types of cattle and antelopes. Among the five primitive species of mastodons there is recorded an animal which resembles and is referred to the typical *Trilophodon angustidens* of the Lower and Middle Miocene of Europe. There is also the trilophodont mastodon (*T. pandionis*) and the more progressive tetralophodont species (*T. perimensis*); it will be recalled that this animal is in a stage of mastodon development which occurs only in the Upper Miocene of Europe. Two forms of *Dinotherium* are recorded in the Lower Manchhar Beds. Among the more rare animals mentioned by Blanford[3] on somewhat doubtful evidence are the scaly anteaters, or

[1] Pilgrim, G. E., Description of Some New Suidæ from the Bugti Hills, Baluchistan. *Rec. Geol. Surv. India*, Vol. XXXVI, Pt. 1, Nov. 1907, pp. 45–56.

[2] The "Javan Rhinoceros" (*R. sondaicus*) now occurs in northern India, Burmah, the Malay Peninsula, Java, Sumatra, and probably Borneo.

[3] Blanford, W. T., 1885, *op. cit.*, p. 37.

pangolins (*Manis*), relatives of which, it will be recalled, first occur in the Oligocene of Europe.

The interpretation of this Lower Manchhar and Bugti fauna as a whole is that it was collected from a forested region not inhabited by grazing types, that it contains some survivals of European browsing types of Oligocene and Lower Miocene age, and that it is chiefly of Middle and partly of Upper Miocene age.

III. MIOCENE LIFE OF NORTH AMERICA

The greatest progress in recent years in American palæontology is in the revelation of the different phases of the Middle and Lower Miocene

FIG. 137. — Chief Miocene and Lower Pliocene fossil mammal deposits of western North America. **1**. Typical Arikaree Formation, S. Dak., Nebr., Col. **2**. Laramie Peak, Wyo. **3**. Pawnee Creek Beds, Col. **4**. Panhandle Beds, Tex. **5**. Deep River Beds, Mont. **6**. Madison Valley Beds, Mont. **7**. Mascall Formation, Oreg. **8**. Republican River, Kan., Nebr. **9**. Santa Fe Marls, N. Mex. **10**. Clarendon Beds, Tex. **11**. Elephas imperator Beds, Tex. (See text for horizons.)

and their relation to the Oligocene. We owe this chiefly to the explorations and studies of Scott, Matthew, Hatcher, and Peterson.

No sudden geologic or life break occurs in America to separate Oligocene from Miocene times, such as that which so sharply demarcates these

periods in Europe; nor, again, can we at present sharply define either the beginning or the close of the American Miocene by comparison with Europe, because the similar animal forms are but few. Nor is there a division of the American Miocene into an older and a newer fauna such as occurs in Europe (p. 249), yet we can make a broad faunistic correlation between the two countries, as follows:

The *older Miocene* in both countries marks the disappearance or absence of some of the most characteristic Oligocene ungulates, such as the entelodonts, or giant pigs, and the dicerathere rhinoceroses. It marks the continued prevalence of browsing herbivorous quadrupeds with short-crowned teeth.

The *newer Miocene* marks the world-wide prevalence of the first grazing horses and other quadrupeds with long-crowned grinding teeth; also of mastodons with trilophodont or three-crested intermediate molars, as well as of mastodons with tetralophodont or four-crested intermediate molars.

Periods	Formations	Horse Zones
Upper Miocene	Ogallala, "Loup Fork," Clarendon, Madison Valley	Hipparion Protohippus
Middle Miocene	Deep River, Pawnee Buttes	Merychippus
Lower Miocene	Arikaree (='Upper Harrison' and 'Upper Rosebud')	Parahippus

Thus the transition in North America from Oligocene to Miocene times is still undetermined, and the line of demarcation adopted in this volume is provisional. The rate of evolution does not help us, because some groups of American mammals evolve more rapidly than corresponding Old World forms; for example, the canids, mustelids, leporids, and the equines. On the other hand, the American geologic stage we have here selected as Lower Miocene does not surely contain either the mastodons, the teleocerine rhinocèroses, or the earliest horned deer so distinctive of the Lower Miocene of Europe; our interpretation is that these animals during Lower Miocene times were slowly migrating and spreading from Europe and Asia into North America, so that they first surely appear in what we call the Middle Miocene. The line of transition between the American Oligocene and Lower Miocene is that indicated as follows:

Transition to the Lower Miocene in the Arikaree (='Upper Harrison,' 'Upper Rosebud') Formations

Mammals characteristic of the Upper Oligocene, absent or undiscovered here	*New mammals characteristic of the Lower Miocene*
Entelodonts	*Mastodon*, evidence doubtful
Hypertragulus	*Blastomeryx*, a cervid
Syndyoceras	*Merycochœrus*, a Miocene oreodont
Steneofiber (last appearance)	*Merychyus*, a Miocene oreodont
Diceratherium	*Phlaocyon*, the first procyonid

Thus, as shown in the accompanying sections of the Pine Ridge (Fig. 138), of Sioux County, Nebraska (Fig. 99), the Arikaree, 'Upper Harrison,' and 'Upper Rosebud' beds, while geologically continuous with the Harrison, and showing no unconformity or other evidence of a break in time, yet do lack some of the mammals found in the Harrison and do

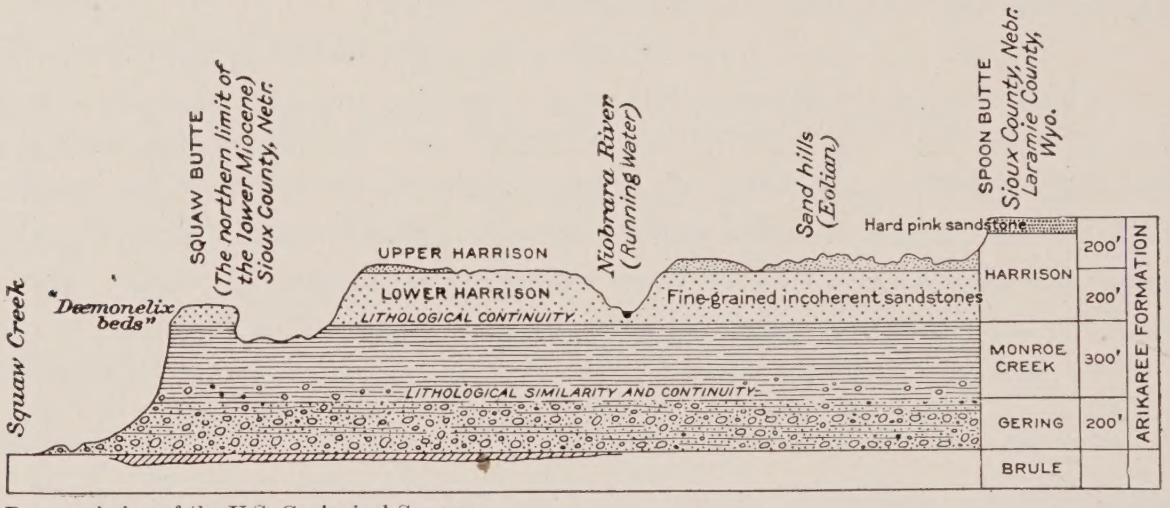


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FIG. 138. — Diagrammatic section of the Lower Miocene. Taken near Harrison, Nebraska. After Peterson.

contain some new mammals not found below. There are proofs of a long interval of time, of several extinctions, and of some quite profound changes of environment and of evolution. Further exploration may modify this artificial line, and either lessen or intensify it.

ANCIENT PHYSIOGRAPHIC CONDITIONS

The Plains Region

Geologic conditions. — The conditions of deposition of these upper beds east of the Rocky Mountains indicate the continuance of the same physiographic features, namely, of great flood plains with a gentle slope in an easterly direction, traversed here and there by river channels containing coarser deposits. The typical Arikaree Formation of Darton,[1] as observed at Pine Ridge in northern Nebraska in 1899, is in the same region as the 'Rosebud' of Matthew. He observes (p. 176) that a large portion of the high lands of western Nebraska and southeastern Wyoming extending from Pine Ridge is occupied by the sands and soft sandstones of the Arikaree Formation. It attains a thickness of over 800 feet in southeastern Wyoming, and formerly extended far up the slopes of the mountains to the north and west. As thus defined, the Upper Harrison of Hatcher, and Upper Rosebud correspond to the upper part of the Arikaree Formation of Darton.

[1] Darton, N. H., Preliminary Report on the Geology and Underground Water Resources of the Central Great Plains. *U.S. Geol. Surv., Prof. Paper*, no. 32, 1905, p. 174.

Hatcher [1] compares the conditions which led to the formation of these great deposits with those at present prevailing along the Parana and Paraguay rivers in South America. Citing from Mr. H. H. Smith, he says: "The flood plain of the Paraguay has a width of one hundred and fifty miles, which broadens as we ascend the river, so that the flood plains of the Upper Paraguay, Amazon, and Orinoco rivers are confluent, and that a vast region about the headwaters of these streams presents similar physical conditions. Here," observes Hatcher, "we have a region of equal or greater area than that occupied by Miocene deposits of our western plains, with all the conditions necessary for the deposition and present distribution of the sandstones, clays, and conglomerates, together with the preservation of remains of the faunas characteristic of each."

The geology of the Lower, Middle, and Upper Miocene formations in Nebraska, South Dakota, Wyoming, Colorado, Montana, Oregon, and Texas still requires further working out. The section taken by Gidley [2] on the Llano Estacado or Staked Plains of Texas (Fig. 167) illustrates how, through the shifting of streams, old formations begin to be worked over into new. Thus the Upper Oligocene Brule Clays are invaded by Lower Miocene streams of the Arikaree; Middle Miocene formations break down to form materials for Upper Miocene (Fig. 167), and in turn all these older formations may contribute to the subsequent Pliocene and Pleistocene. In general the Miocene overlaps the Oligocene eastward and extends south into Texas and north into Montana. To the north it is much cut up by erosion, to the south and east much buried by later sediment. It is largely composed of altered or eroded volcanic ash materials; in some places pure volcanic ash beds are found. The general direction of the streams was from west to east, or from the mountains out upon the plains. Thus the Miocene becomes finer and thinner as we proceed eastward, while the coarse materials and sedimentary sands and clays are found closer to the mountains. To a certain extent the evidence points to the same east and west stream channels as exist to-day.[3]

The Mountain Region

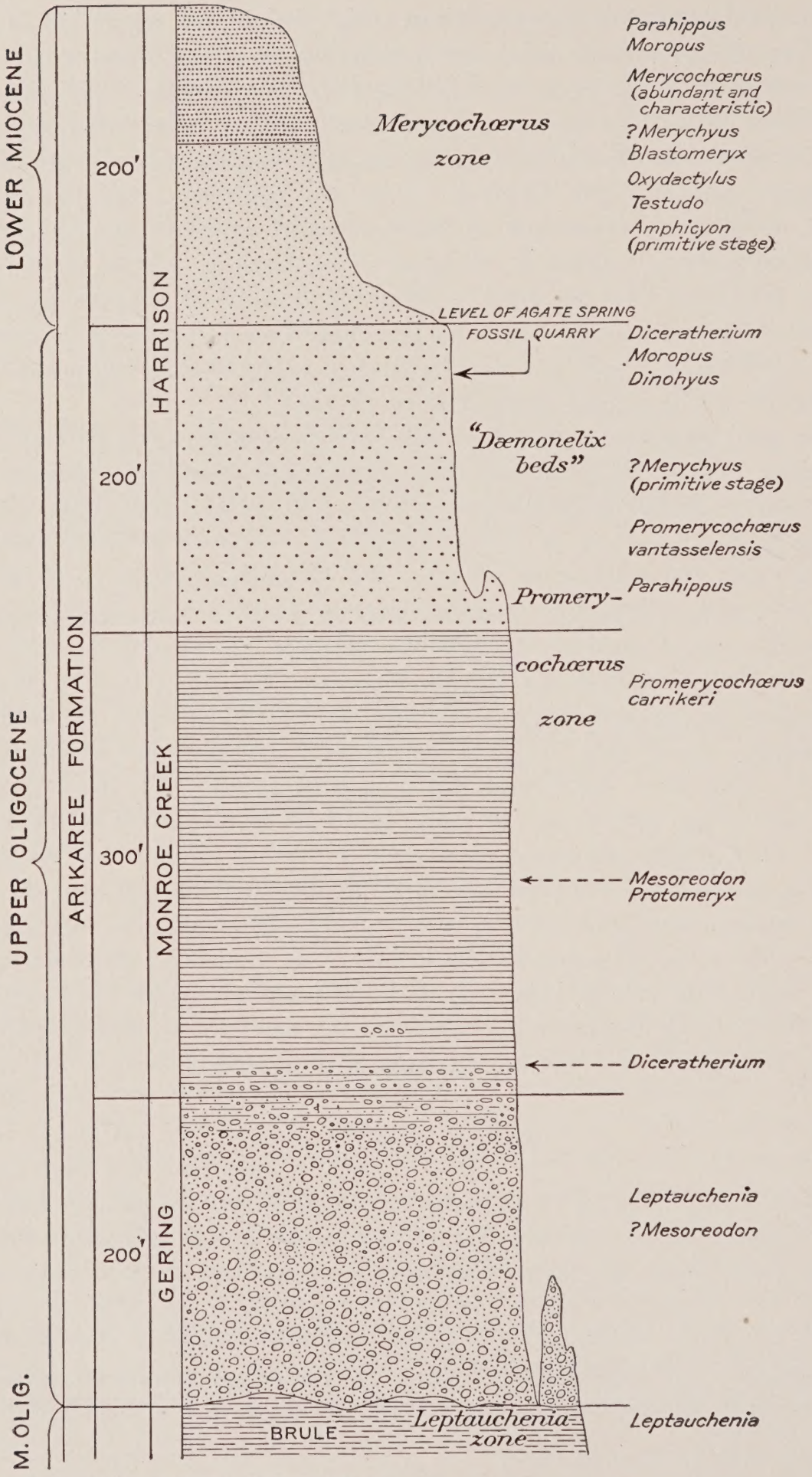
Oligocene and Miocene of Montana.[4] — In Montana the Rocky Mountain chain extends far to the west, and with it the outlying Tertiaries. The ancient flood plain and lacustrine deposits occupy the large valleys of the

[1] Hatcher, J. B., Origin of the Oligocene and Miocene Deposits of the Great Plains. *Amer. Philos. Soc. Proc.*, Vol. XLI, 1902, pp. 113–131.

[2] Modified (1908) from section in: Gidley, The Fresh-water Tertiary of Northwestern Texas, American Museum Expedition, 1899–1901. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX, 1903, pp. 617–635.

[3] From notes by W. D. Matthew.

[4] Douglass, The Neocene Lake Beds of Western Montana and Descriptions of Some New Vertebrates from the Loup Fork. *Univ. Montana*, thesis, June, 1899.



By permission of the U.S. Geological Survey.

FIG. 139. — Scale section corresponding with section A near Harrison in Fig. 99. After Peterson.

upper Missouri east of the Rockies above the region of Helena, especially the Gallatin, Madison, Jefferson, Beaverhead, Ruby, Big Hole, Hell Gate; they extend also along the Bitter Root rivers and their tributaries. Hayden and Peale in 1871 and 1872 gave the first good general description of these deposits in the Annual Reports of the United States Geological Survey of the Territories.

The geologic history of these successive formations differs in one important respect from that of the great plains of Nebraska and South Dakota, because the older Oligocene beds were uplifted in places to a considerable angle (35°) before the Middle Miocene deposits were laid down. Extensive layers of volcanic ash overlie the lower Oligocene beds of the Titanotherium Zone, and the Upper Miocene Madison Valley Formation is partly composed of layers of volcanic ash as well as the 'channel beds' of sand and gravel.

Pipestone Creek. — The oldest mammals of these deposits are those found in the lower beds near the three forks of the Missouri River, on Pipestone Creek near Whitehall and on the Big Hole north of Dillon. These beds consist of gray and yellow clays and sandstones and conglomerates, 200 feet in thickness, containing a lower 'Titanotherium Zone' fauna, namely, of Lower Oligocene age.

Deep River. — Near White Sulphur Springs, also, in the valley of Deep River, there is a comparatively small lacustrine or flood plain deposit, including the 'Lower' and 'Upper' Deep River beds. The 'Lower Deep River beds' contain a fauna of Upper Oligocene age. The prevailing fauna of the overlying, or 'Upper Deep River beds,' which has been described by Cope (1879) and Scott (1893, 1895) is of Middle Miocene age; this is the typical 'Ticholeptus Zone' of Cope. Here we find remains of brachyodont and subhypsodont horses, and of the oreodonts (*Merychyus* and *Ticholeptus*). According to Cope, the *Trilophodon*, among the earliest Proboscidea occurring in America, is found here; Douglass thinks it possible that this type belongs to a more recent formation.

Flint Creek. — Subsequent in age to these three faunas are the mammals of Middle Miocene age contained on Flint Creek and in the lower portion of the valley of the Madison River which united with the Jefferson and Gallatin to form the Missouri.

Madison Valley. — This formation, of true Upper Miocene age, two hundred and fifty feet in thickness, is composed of sands, gravels, clays, and volcanic ash that are often grassed over, covered with drift, or entirely washed away; yet near the Madison River there is one exposure fifteen to twenty miles in extent. It contains hypsodont horses (*Protohippus* and *Neohipparion*), the camel *Procamelus*, the primitive deer *Blastomeryx*, also trilophodont mastodons. Especially important is the ruminant obtained here, originally described by Douglass as *Palæomeryx*, but now referred to *Dromomeryx*.

The Pacific Coast Region

Before the Miocene epoch connection between the Atlantic and Pacific oceans of Eocene times had wholly ceased, and the coast faunas of the later Tertiary were wholly of the Pacific type. The Lower Miocene was still a warm oceanic period; for we find in its fauna a nautilus still persisting, and other genera now found only in southern waters. The accumulation of organic remains along the Coast Range furnishes the series from which the petroleum of California was afterwards distilled. In the northern interior vast outpourings of the Columbian lava flow (see p. 359) which covered an area of more than 200,000 square miles, including the northeastern part of California, occurred about the middle of the Miocene. In the Upper Miocene the climate of California was no longer sub-tropical, but warm-temperate, and most like that of the states bordering the present Gulf of Mexico. Marine animals like those of our time abounded in the waters, and along with them were some southern forms. On the land, elms, walnuts, hickories, and laurels flourished, indicating a temperate, rainy climate, more moist, if not more mild, than that of to-day in the same region. In the Sierra Nevada Mountains of this epoch there were large rivers winding slowly down low grades, overloaded with sediments, the auriferous gravels, which spread out on low plains not far above sea level; through subsequent elevation these flood-plain deposits are now found higher up on the Sierra Nevadas, with their channels buried under later lava flows.[1]

Miocene Flora

Our knowledge of the Miocene flora of North America is confined to that of the ancient forests of the great mountain region, as described chiefly by Knowlton [2] and Cockerell,[3] extending from Colorado northward through Montana, Nevada, Idaho, Oregon, and Washington. The famous 'Mascall' flora of Oregon is of Middle Miocene age; the similar but by no means identical flora of Florissant, Colorado, is of somewhat more recent, perhaps Upper Miocene, age.

In the rich plant beds of the ancient lake deposits of all this region, there is no record of the existence of any palms, although there are occasional tropical plants and many warm temperate forms; yet the proportion of tropical types is much smaller than in the Eocene. Sequoias are less frequent. The horsetails (*Equisetum*) begin to be reduced both in numbers and size. The ginkgo still occurs, although it is less numerous. The figs (*Ficus*) still flourish in Montana, Nevada, Idaho, and Oregon. This gives us a hint as to temperature, for the fig now grows in northern Florida,

[1] Smith, J. P., Salient Events in the Geologic History of California. *Science*, n.s., Vol. XXX, no. 767, 1909, pp. 346–351.

[2] See Knowlton, H. F., 1893, 1896, 1898, 1900, 1902, in Bibliography.

[3] Cockerell, T. D. A., 1906, 1908, in Bibliography.

latitude 30°, and in Europe as far north as the Black Sea, latitude 40°, in a January isotherm of 40° Fahr. to 50° Fahr. (4° C. to 10° C.). In Oregon is recorded *Artocarpus*, the breadfruit, now confined to the Pacific Islands. Magnolias abound through all this region. We infer that in this mountainous, volcanic, and well-forested region the climate was more equable, and south temperate rather than tropical, with abundant moisture, but not continuously humid.

Predominant in the Miocene flora (Mascall) of the mountain region were the following genera:

Willows, *Salix*
Poplars, *Populus*
Sumach, *Rhus*
Walnuts, *Juglans*
Oaks, *Quercus*
Elms, *Ulmus*
Plane trees, *Platanus*
Magnolias, *Magnolia*
Figs, *Ficus*

Less abundant were the myrtles (*Myrica*), birches (*Betula*), alders (*Alnus*), laurels (*Laurus*), staff trees (*Celastrus*), maples (*Acer*), persimmons (*Diospyros*), aralias (*Aralia*), ferns (*Filices*) and horsetails (*Equisetum*).

On the great plains and along the borders of the great rivers which traversed them, the flora probably included types adapted to a warmer temperature. Of these we have no direct knowledge, as no plant beds are preserved. Certainly there is no proof of tropical conditions north of the fortieth parallel.

As for the field flora of the plains an appeal must again be made to the dental anatomy of the mammals, which demonstrates that grasses were constantly increasing and formed the chief food of the prevailing types of horses and ruminants in Upper Miocene times.

Florissant Lake. — The deposits of the ancient lake basin of Florissant, Colorado, now in the heart of the arid region of the Rocky Mountains, elevated to a height of eight thousand feet, were especially monographed by Samuel Hubbard Scudder,[1] and more recently studied by T. D. A. Cockerell,[2] so that we now know the plants of its shores, the insects which hovered about them, and other characteristics which are most significant as to conditions in the border mountain region in Miocene times. The lake lay in a long, narrow valley between granitic mountains, surrounded by volcanoes, so that the very shales in which the remains of plants and insects are entombed are wholly composed of volcanic sand and ash from a source probably close at hand (Scudder, 1890, pp. 18–34). From consideration of all the evidence, Cockerell[3] regards the age of these beds as

[1] Scudder, S. H., The Tertiary Insects of North America. *U.S. Geol. Surv. Terr., Rept.*, Vol. XIII, 1890.

[2] Cockerell, The Fossil Fauna and Flora of the Florissant (Colorado) Shales. *Univ. Col. Studies*, Vol. III, no. 3, Boulder, Col., June, 1906; also, The Fossil Flora of Florissant, Colorado. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, no. 4, 1908, pp. 71–110; and, The Miocene Trees of the Rocky Mountains. *Amer. Natural.*, Vol. XLIV, no. 57, January, 1910, pp. 31–47.

[3] Cockerell, letter to the author, March, 1908.

probably Upper rather than Lower Miocene. Both the plants and insects show a very close general correspondence with those of Œningen as described by Heer,[1] and Œningen is now considered (p. 263) Middle Miocene. The plants of Florissant are in general similar to those of the Colorado uplands and of our southern states; they are in no sense tropical, and there are no palms whatever. Of the more than hundred genera described, many still exist in Colorado, such as pines (*Pinus*), 'cedars' (*Sabina*), alders (*Alnus*), oaks (*Quercus*), rose (*Rosa*), ash (*Fraxinus*), grape (*Vitis*), maple (*Acer*), sumac (*Rhus*), thorn (*Cratægus*), thistle (*Carduus*), aster (*Aster*), Virginia creeper (*Parthenoçissus*). It would be easy by selection of a large series of such plants and also insects, so similar to those of modern Colorado, to conclude that since the Miocene there had been no climatic changes of any moment. Thus the narrow-leafed cottonwood (*Populus*) is almost exactly like the common tree of the Colorado foothills; and many other examples might be cited.

On the other hand, mixed with this familiar flora is a very different one, indicative of a warmer, moister climate. The most prominent element of this other flora is the southern one, such as is found in the eastern United States to-day, including several species of the soapberry (*Sapindus*), sweet fern (*Comptonia*), sweet gum (*Liquidambar*), two kinds of chestnut (*Castania*), basswood (*Tilia*), several species of holly (*Ilex*), smoke tree (*Cotinus*), persimmon (*Diospyros*), and even one or two of the figs (*Ficus*). This flora, however, is not one of the extreme south.

Other elements in the flora are of minor importance, but include the giant redwood (*Sequoia*) now of California. With it grew an incense cedar (*Heyderia*), now found in America only on the Pacific coast; it also survives (a single species) in Asia. The sequoia and incense cedar are both very closely related to their living Californian allies. Several species of *Weinmannia* represent a shrub still extant in the mountains of the West Indies. The Old World genera of Florissant, not found in America at all to-day, are few and mostly of doubtful identification; perhaps the best case is that of *Porana* of the order Convolvulaceæ, now living in the East Indies and fossil also in the European Miocene. "So far as I am able to judge," continues Dr. Cockerell,[2] "the insects tell the same tale as the plants, except that the Old World element is much more definite and indisputable, though small." The most striking members of this Old World group are two species of the tse-tse fly (*Glossina*), to-day exclusively African; this is of especial interest in connection with the introduction of African mammals (*Mastodon*) into the Miocene of North America. One of the orthopterous insects, a sort of large grasshopper, shows resemblances to a living African genus. Certain neuropterous insects, resembling the 'ant-

[1] Heer, O., Flora tertiaria Helvetiæ, Winterthur, 1853–1859; also, Die Urwelt der Schweiz, 2d. ed., Zürich, 1873.

[2] Letter to the author, March, 1908.

lions,' belong to a family now extinct in North America, but represented in Chili, in Persia, and abundantly in Africa. Two species of the horse fly (*Tabanus*) are also found here, quite close to living forms. It is interesting to note that while the Equidæ have undergone generic changes since Miocene times, their tormentors have remained not only generically the same, but have changed little specifically.[1] The now extinct element in the insect fauna includes certain plant lice, dragon flies, and cicadas. The Neotropical or South American element, if there be any, must be slight.

"From consideration of all the evidence," continues the same writer, "I conclude that the climate of Florissant at the time the shales were deposited was warm and moist, but in no sense tropical, the flora including a hilly and lake border element. The altitude was not much less than it is to-day (8,000 feet), but under the prevailing climatic conditions there were no heavy winter snows. There is apparently no reason why these moist mountain side conditions of the Florissant Lake should not have been contemporaneous with the presence of arid conditions in Texas, Kansas, and the great plains generally."[1]

The horse flies of Florissant are especially interesting in connection with the epidemic theory of extinction of some of the American mammals, suggested by Osborn[2] and others. The deadly nature of the tse-tse fly (*Glossina*) in Africa is well known. In Algeria the tabanids also transport a trypanosome disease of the dromedary. It seems possible, therefore, that both these flies may have been instrumental in carrying diseases to the Mammalia.[3]

Lower Miocene

Merycochœrus Zone

Geologic distribution. — As described above on p. 279, the geographic area in which these mammals are known is identical with that of the close of the Oligocene because it is revealed in a continuation of the upper portions of the Upper Oligocene, Arikaree, Harrison, and Rosebud Formations of western Nebraska and South Dakota, also farther west around the base of Laramie Peak, and to the south in the uppermost Martin Cañon of Colorado. Our knowledge is again due chiefly to the comparatively recent explorations and studies of Peterson, Matthew, Cook, and Thomson.

There is no foreign invasion. The mammal fauna is entirely American, that is, derived from American Oligocene ancestors. A possible exception is indicated by a portion of two teeth which remotely resemble those of one of the primitive mastodons; we await further evidence on this point.[4]

[1] Cockerell, Letter to the author, March, 1908.

[2] Osborn, H. F., The Causes of Extinction of Mammalia. *Amer. Natural.*, Vol. XL, no. 479, 1906, pp. 769–795, no. 480, pp. 829–859.

[3] Cockerell, Letter to the author, Jan. 9, 1909.

[4] Cook, Harold J., A New Proboscidean [*Gomphotherium conodon*] from the Lower Miocene of Nebraska. *Amer. Jour. Sci.*, Vol. XXVIII, Aug., 1909, pp. 183–184.

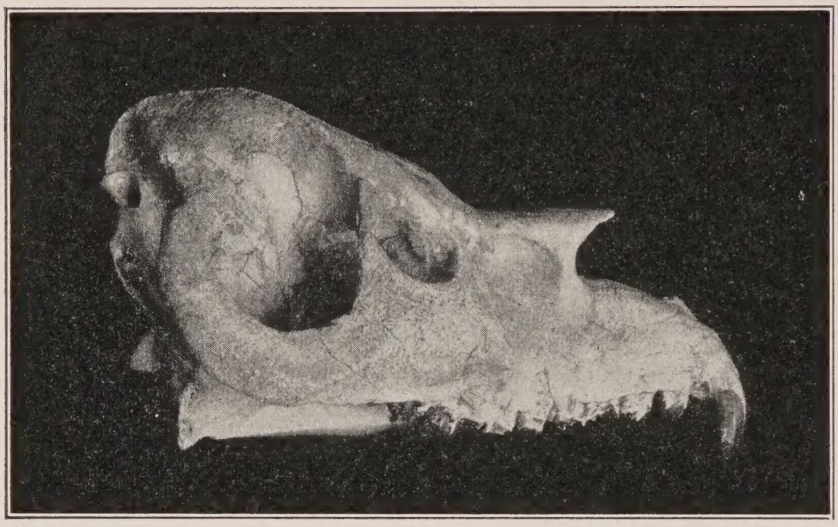


FIG. 140. — Skull of the typical Lower Miocene oreodont *Merycochœrus proprius*. In the American Museum of Natural History. After Matthew.

The fossils are, however, less abundant than in the lower horizon, and further exploration is awaited with interest. As observed on p. 277, in defining these beds as Lower Miocene the following characteristic Oligocene forms are now believed to be absent: *Entelodon* (*Dinohyus*), *Hypertragulus*, and *Steneofiber*. The latter genus is replaced in Europe by the Lower Miocene *Chalicomys;* its successors in America are perhaps the Upper Miocene and Pliocene *Hystricops* and *Eucastor*.

LOWER MIOCENE

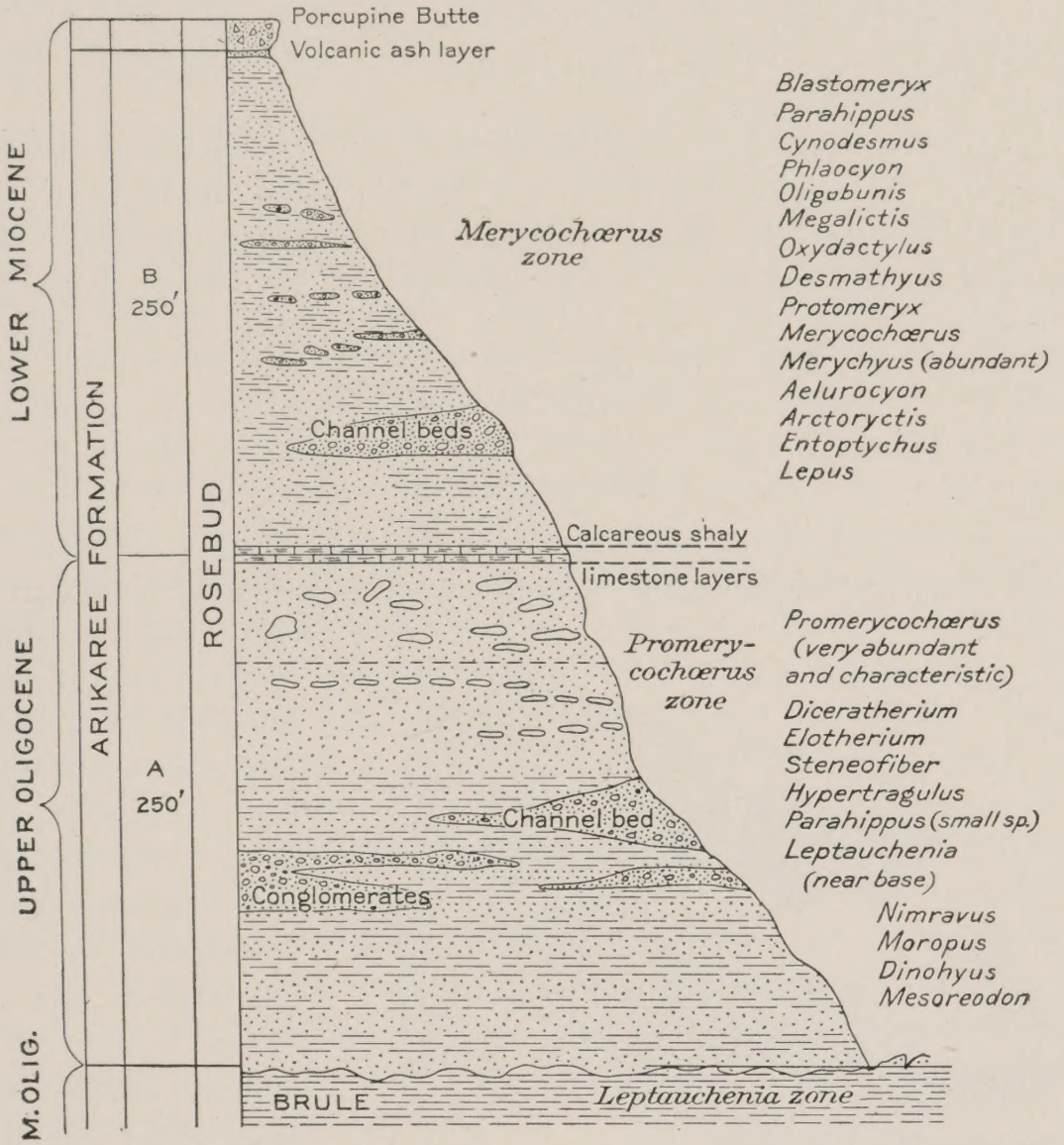
?Mastodons
Camelids
  Protomeryx
  Oxydactylus
Oreodonts
  Merycochœrus
  Merychyus
Pro-Cervids
  Blastomeryx
  (hornless)
Horses
  Parahippus
  ?Altippus
Rhinoceroses
  Aceratherium
  Diceratherium
Procyonids
  Phlaocyon
Mustelids
  Megalictis
Rodents

Especially noteworthy among the new Lower Miocene mammals is *Blastomeryx*, a descendant of the Oligocene *Leptomeryx*, and broadly ancestral to the American deer (*Mazama* and *Odocoileus*). This animal is hornless but provided with sharp canine tusks, and is in the same stage of evolution as *Dremotherium* of the Upper Oligocene of Europe. Other new artiodactyls are the oreodonts *Merycochœrus* and *Merychyus*. The former is a brachycephalic, or short-faced successor of *Promerycochœrus*, while *Merychyus* is a smaller animal which becomes extremely abundant and is especially characteristic of the Middle Miocene. Both these oreodonts persist through the Miocene. Among the tylopods or camelids the long-limbed and long-necked *Oxydactylus* [1] again appears, a tree-browsing camel with brachyodont molar teeth broadly ancestral to the 'giraffe camels' of the Middle and Upper Miocene. The other camelid, *Protomeryx*, was a small, rather short-limbed animal with hypsodont molars; it probably gave rise to the line of camels that ended in the Pleistocene with very large and long-limbed forms. The peccaries are again represented in *Desmathyus*.

The perissodactyl Herbivora include the chalicotheres (*Moropus*) and the last survivors of the

[1] Peterson, O. A., Osteology of Oxydactylus. *Ann. Carneg. Mus.*, Vol. II, no. 3, Feb., 1904.

diceratheres. The horses are becoming more varied, including *Parahippus* (*P. nebrascensis*) as well as an extremely light-limbed form, possibly similar to the *Altippus* described by Douglass[1] from the Lower Miocene Fort Logan Formation of Montana; this is an equine which combines brachyodont molar teeth with long and very slender limbs and feet. There are



By permission of the U.S. Geological Survey.

FIG. 141. — Scale section of the Rosebud Formation. After Thomson and Matthew.

also more diminutive horses, scarcely exceeding in size the Oligocene *Mesohippus*. All these horses have short-crowned molar teeth.

Of the rodents all the Oligocene families continue, and Matthew finds evidence of the occurrence of the heteromyids, the leaping rodents related to the existing *Heteromys*, which is in the same family with the 'American kangaroo rat' or *Dipodomys*. Especially interesting is the occurrence of a new insectivore, *Arctoryctes*, doubtfully related to the South African chrysochlorids, or Cape Golden moles.

Of the Carnivora the felids of this stage still await discovery. The

[1] Douglass, E., Fossil Horses from North Dakota and Montana. *Ann. Carneg. Mus.*, Vol. IV, nos. 3 and 4, 1908.

canids, represented by *Cynodesmus*, are abundant and varied. This is the first geological appearance of the characteristically American family of raccoons, or procyonids, here represented by *Phlaocyon*. The Mustelidæ are represented by the Oligocene *Oligobunis* and two new forms of superior size (*Ælurocyon* and *Megalictis*); the latter (*M. ferox*) is a very powerful mustelid, intermediate in character between the ratel (*Mellivora*) of Africa and India and the wolverine (*Gulo*), an animal which subsequently becomes Holarctic in distribution.

It is striking that every representative of the Testudinata found in the Arikaree, or 'Upper Harrison' beds is an upland form, and so far as known all remains belong to the genus *Testudo*, which embraces the land tortoises, represented by five species. This is suggestive of the æolian deposition of these beds.[1]

Middle Miocene

Ticholeptus Zone

Deep River and Flint Creek, Montana; Mascall, Oregon; Pawnee Creek, Colorado. — In the above-named formations of Montana, Oregon, and Colorado, which are broadly united as the *Middle Miocene* or *Ticholeptus Zone*, we meet another very profound change in the mammalian life of North America, which corresponds to that occurring in the *Lower Miocene* of Europe, namely, the first appearance both of the African mastodons and of the short-limbed rhinoceroses, or Teleocerinæ. It is supposed that these Lower Miocene invaders of Europe reached America in the Middle Miocene, but it is quite possible that future discovery may give a greater age to these formations. Another resemblance to the Lower Miocene of Europe is the occurrence at this level of the earliest horned or antlered ruminants. These, however, have no known European affinities, since they

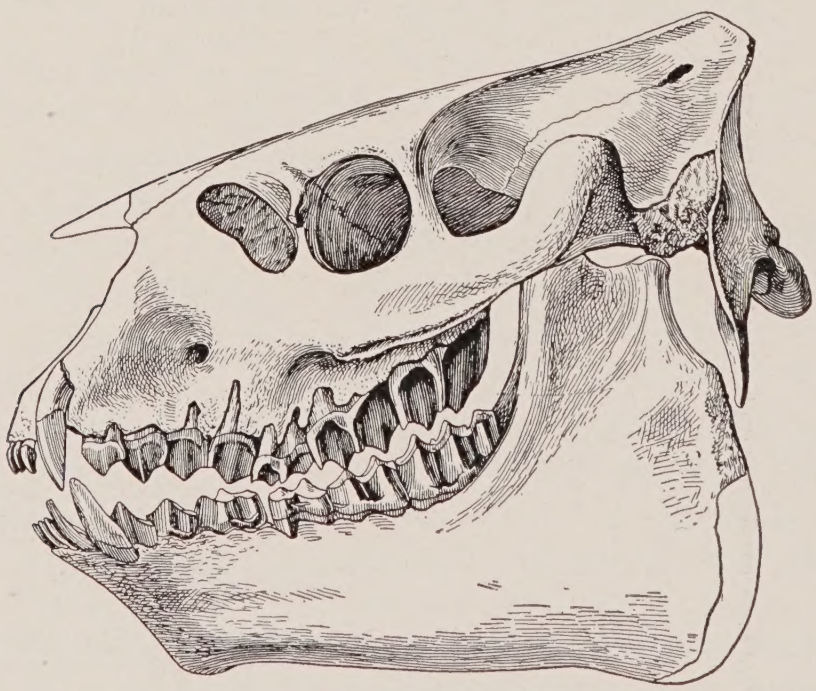


Fig. 142. — Skull of the typical Middle Miocene oreodont *Ticholeptus breviceps* Douglass (Type), about $\frac{3}{8}$. After Douglass.

[1] Loomis, F. B., Turtles from the Upper Harrison Beds. *Amer. Jour. Sci.*, Vol. XXVIII, no. 163, July, 1909, pp. 17–26.

belong to the peculiarly American family of Miocene and Pliocene merycodonts, allied in skeletal but not in horn structure to the modern prong-horned antelopes or antilocaprids.

The appearance of these modernized selenodont artiodactyls or Pecora must have effected a change in the external aspect of the fauna only less marked than that caused by mastodons and bulky rhinoceroses. Other new elements of Eurasiatic origin appear. Among the artiodactyls appears a bovine or antelopine form somewhat similar to the characteristic *Protragocerus* of the Middle Miocene of Europe, an animal (*Dromomeryx*) whose zoölogic position is still uncertain; it presents certain resemblances to the Antilocapridæ. There are also carnivores resembling the amphicyons, and among the Mustelidæ the otters appear (*Potamotherium*), animals which are first recorded in the Upper Oligocene or Aquitanian of Europe. A felid similar to the characteristic Lower Miocene *Pseudælurus* also occurs.

Probably of native or North American origin, because related to the haplodontids or sewellels, is a very peculiar family of mylagaulid rodents with short, deep skulls, but which depart from all other rodents in developing horns.

Most surprising is the evidence of the existence of true edentates of *Megalonyx* type in the Mascall beds of Oregon.[1] The extinction of several mammals characteristic of the Lower Miocene or *Promerycochœrus* Zone, and the occurrence of more advanced stages in the evolution of the horses and camels, especially mark this stage as intermediate or halfway between Lower and Upper Miocene.

Formations. — The Deep River, or Ticholeptus Zone of Oregon was discovered by Grinnell and Dana in 1875, and divided into two levels by Cope in 1879, namely, the Ticholeptus and Procamelus beds (Upper Miocene) which he rightly recognized as quite distinct in age. In 1893 Scott first fully characterized the mammals of these beds, and concluded that the nearest European equivalent is the fauna of Sansan and Simorre,[2] which we now determine as Middle Miocene.

The Pawnee Creek horizon of Colorado was first explored by Cope in 1873. The American Museum parties entered these beds in 1898, and returned in 1901, under Matthew, who first distinguished the horizon from the 'Loup Fork,' or Upper Miocene, to which all previous writers had referred it.[3] In 1903 Douglass[4] made known the mammals of the Flint Creek Formation in Montana, which proved to be of similar age, or transi-

[1] Sinclair, W. J., Some Edentate-like Remains from the Mascall Beds of Oregon. *Univ. Cal., Bull. Dept. Geol.*, Vol. V, no. 2, 1906, pp. 65–66.

[2] Scott, W. B., The Mammalia of the Deep River Beds. *Trans. Amer. Philos. Soc.*, n.s., Vol. XVIII, 1895, no. 2, p. 182.

[3] Matthew, W. D., Fossil Mammals of the Tertiary of Northeastern Colorado. *Amer. Mus. Nat. Hist.*, Mem. I, Pt. 7, Nov., 1901, pp. 358–374.

[4] Douglass, E., The Neocene Lake Beds of Western Montana, and Descriptions of Some Vertebrates from the Loup Fork. *Univ. Montana*, thesis, June, 1899.

tional to the Upper Miocene. Finally the studies of Merriam[1] and Sinclair[2] have confirmed Cope's opinion that the Mascall of Oregon, immediately overlying the Columbia River lava which caps the Upper Oligocene of the John Day Formation, is also of this age. The Virgin Valley of Nevada (p. 356) has recently yielded a fauna of similar age. We are thus enabled to again survey the mammalian life of North America over a wide geographic area extending from the plains to the mountain region, and on the whole very uniform in character. As bearing upon the climate of

FIG. 143. — Middle Miocene of Colorado. A view of West Pawnee Butte, taken from the summit of East Pawnee Butte. Photograph by American Museum of Natural History expedition of 1901.

these times it is interesting to observe the testimony of the Mascall flora, as described by Knowlton.[3]

Flora of the northwest mountain region. — In the northwest mountain region no palms are recorded (cf. pp. 282–4). The vegetation still bore a southern character. The Mascall flora of the John Day Basin (lat. 45° N.), which is regarded as Middle Miocene, is relatively rich. It was distinctly a hard wood flora, in general appearance like that of the area east of the Mississippi at the present time.[4] There were large numbers of horsetails (*Equisetum*), but the ferns were scarce. Both of the grasses (Gramineæ)

[1] Merriam, J. C., A Contribution to the Geology of the John Day Basin. *Univ. Cal., Bull. Dept. Geol.*, Vol. II, 1901.

[2] Sinclair, W. J., Some Edentate-like Remains from the Mascall Beds of Oregon. *Univ. Cal., Bull. Dept. Geol.*, Vol. V., no. 2. 1906, pp. 65–66.

[3] Knowlton, F. H., Fossil Flora of the John Day Basin, Oregon. *U.S. Geol. Surv.*, Bull., 204, 1902.

[4] *Ibid., p.* 93.

and the sedges (Cyperaceæ) only a single doubtful form has been found. The conifers, although represented by several genera, must also have played an inconspicuous rôle. Of the deciduous types, the birches (Betulaceæ) were most abundant; next in importance were the beeches (Fagaceæ), and then the maples (Aceraceæ), which attained a great size in the Mascall

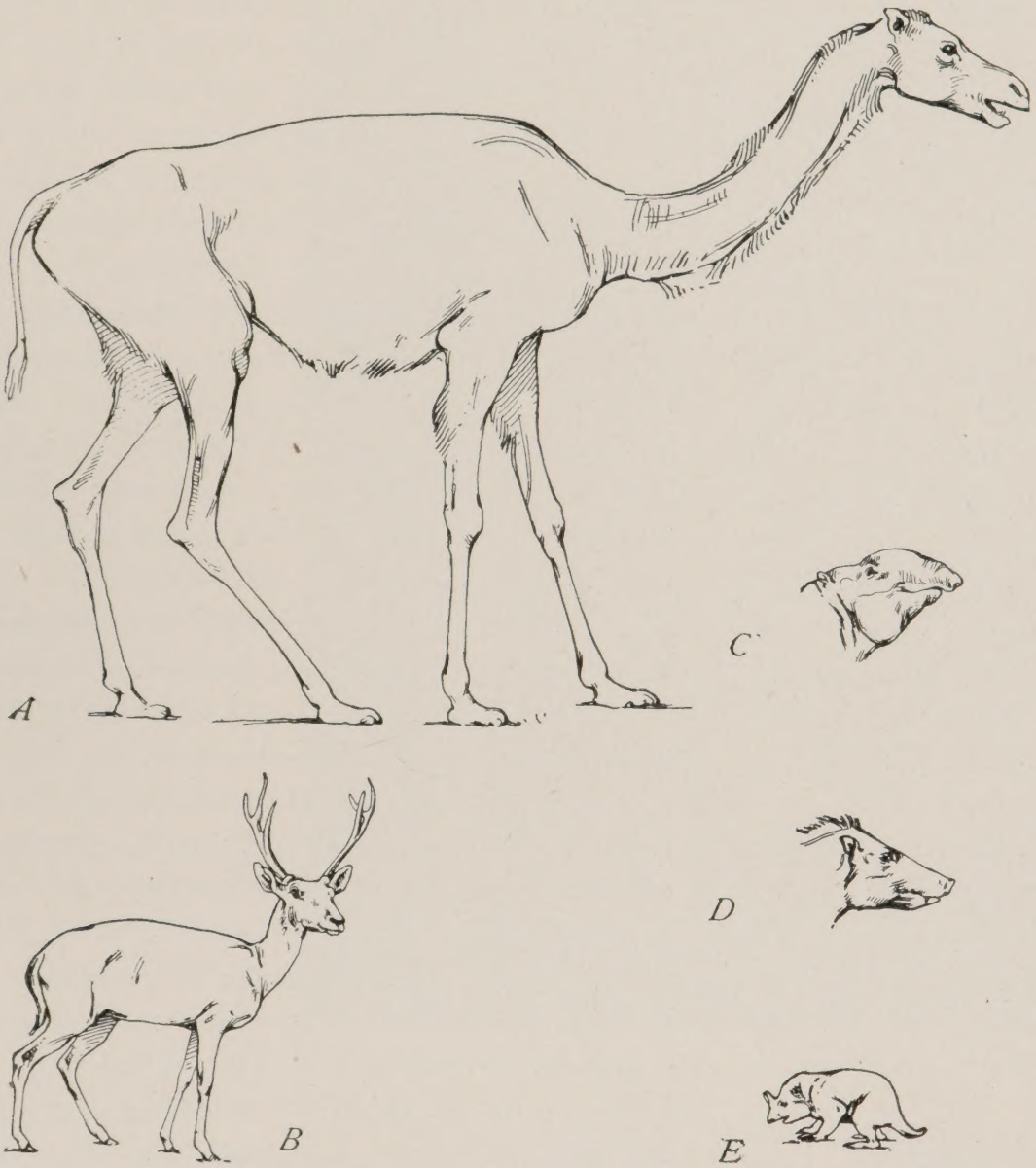


FIG. 144. — Contemporary Middle Miocene mammals of the western plains region to same scale ($\times \frac{1}{24}$). By Charles R. Knight. *A. Oxydactylus*, primitive giraffe camel. *B. Merycodus*, ancestral horned ruminant. *C. Pronomotherium*, aquatic oreodont with proboscis. *D. Thinohyus*, ancestral peccary. *E. Epigaulus*, horned burrowing rodent.

beds. We observe also walnuts, plane trees, willows, and sweet gums, the latter (*Liquidambar*) forming a conspicuous element. Dr. Arthur Hollick[1] observes of this flora of central Oregon in Middle Miocene times that it points to a temperate climate, the breadfruit (*Artocarpus*) alone indicating warmer conditions, although both this form and the alleged cinnamon (*Cinnamomum*) are not certainly identified. The climate was probably south temperate.

[1] Notes by Dr. Hollick, March, 1909.

Fauna. — The conspectus of the fauna exhibits at once its wide departure from the Upper Oligocene and its successive Lower Miocene stages as above described.

Proboscideans
  Trilophodon
Rhinoceroses
  Teleocerine
  Aceratherine
Horses
  Merychippus stage
  Hypohippus stage
Tapirs
Chalicotheres
Peccaries
Oreodonts
  Ticholeptus stage
Camelids
  Protolabis stage
  Alticamelus stage
Palæomerycines
  Dromomeryx
Merycodontids
  Merycodus
Edentates
  Megalonychids
Canids
Amphicyonids
Mustelids
  Otters
Felids
  Pseudælurus
Mylagaulids

The reported occurrence of edentates of the gravigrade type is especially interesting because these animals were supposed to have first invaded North America in Middle Pliocene times. It must be remembered that the occurrence of armadillo-like forms in the Bridger (p. 164) points to the possibility that the edentates were resident in certain parts of North America from early times.

The occurrence of gravigrade sloths in the Miocene of the northwest seems consistent with Scharff's theory that North and South America were at times connected through Lower California and western South America.[1] But this theory is inconsistent with the fact that other animals did not pass south or north.

The Proboscidea are relatively little known, being represented by two species (*T. proavus*, *T. brevidens*), neither of which has the long, narrow grinding teeth characteristic of *T. angustidens* of the Lower Miocene of Europe. Of the rhinoceroses the species *Teleoceras medicornutus*, discovered in the Pawnee Creek region of Colorado, is a remarkably close successor of the *T. aurelianense* of the Lower Miocene of France, because both possess beside the terminal nasal horn a rudimentary frontal horn. This is one of the most brilliant illustrations of the migration theory between the New and Old Worlds. Of the aceratherine rhinoceroses, which are best known in the plains region of Colorado, the type of Cope's genus *Aphelops* (*A. megalodus*) occurs at this level.

Of the browsing, or leaf-eating fauna, we find three important examples among the horses, namely, *Hypohippus* of Oregon and Colorado, a supposed forest-living horse with short-crested teeth and persistent tridactyl feet, *Archæohippus* of the Mascall, Oregon, a small animal with teeth resembling those of the Oligocene *Mesohippus*, but distinguished by two very large preorbital pits; and the short-crowned *Parahippus* (=*Desmathippus* Scott), in which, although the molars are brachyodont, a fine deposit of cement

[1] Scharff, R. F., On an Early Tertiary Land-connection between North and South America. *Amer. Natural.*, Vol. XLIII, Sept. 1909, pp. 513–531.

appears in the valleys. Of these several phyla of horses the *Hypohippus* is closest to the Middle Miocene *Anchitherium* of Europe; in fact, it was believed by Scott[1] to belong to this genus. Widely distinguished by its elongate or sub-hypsodont molar teeth is the plains-living, probably grass-eating horse *Merychippus* of Colorado, certain species of which lead into the true equines or Hippotheriinæ.

The tapirs are still sparingly represented in the remains of advanced types.

Dominant members of the artiodactyl fauna are the oreodonts and camelids, both of which show a high degree of adaptive radiation. Among the oreodonts *Merycochœrus* and *Merychyus* persist. *Promerycochœrus* is again abundant in the Deep River beds of Montana. The very characteristic and widespread genus *Ticholeptus* is probably a direct and slightly modified descendant of *Eporeodon* of the summit of the Oligocene, while the small and extremely broad-skulled *Cyclopidius* suggests *Leptauchenia* of the Upper Oligocene.

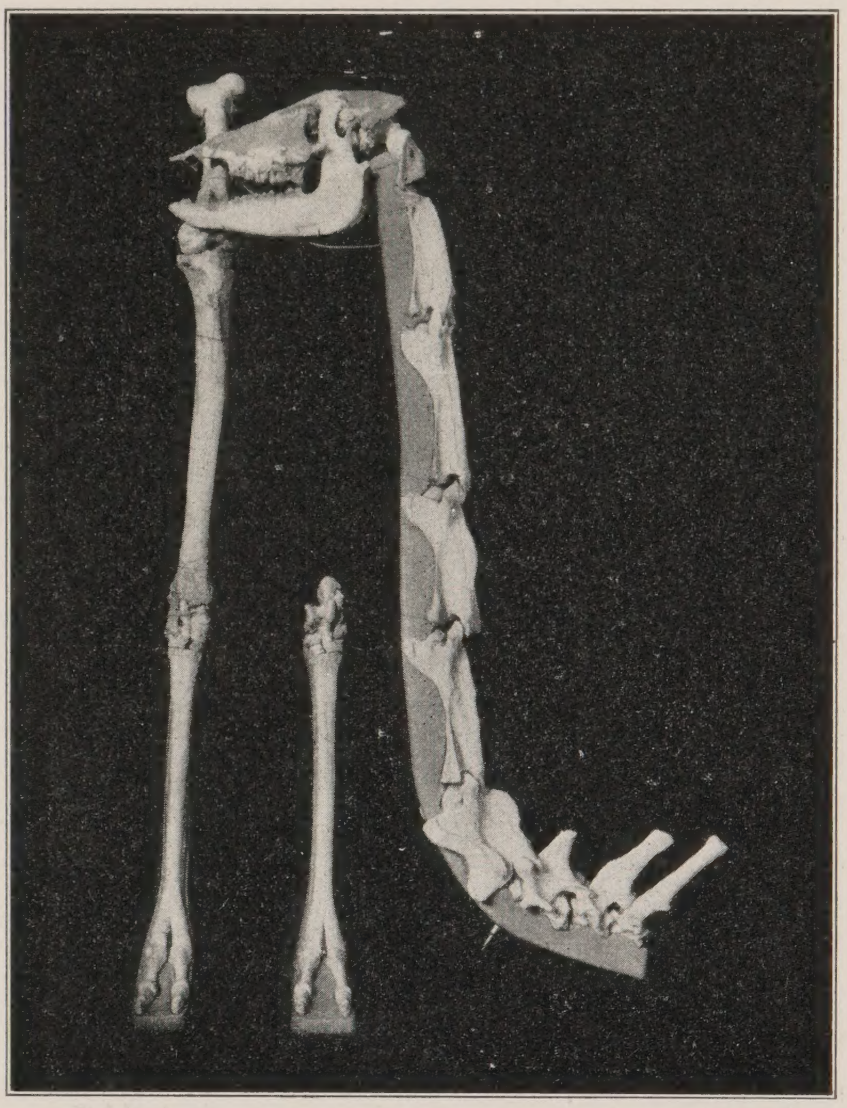


Fig. 145. — Skull, neck, and limbs of the large Middle Miocene "giraffe camel," *Alticamelus altus*, of Colorado. In the American Museum of Natural History. After Matthew.

The camels are now still more clearly divided into the browsing types with short-crowned teeth, and the grazing types with long-crowned teeth. Among the former the remarkable 'giraffe camel' *Alticamelus* replaces *Oxydactylus* of the Lower Miocene. The recognition by Matthew[2] of this parallel with the Old World giraffes was a most interesting contribution to the Miocene zoölogy of America. The existence of long-limbed, long-necked, brachyodont types of camels browsing from the

[1] Scott, W. B., Mammalia of the Deep River Beds, 1895, p. 181.

[2] Matthew, W. D., Fossil Mammals of the Tertiary of Northeastern Colorado, 1901.

tops of trees is conclusive evidence of increasing arid conditions and lengthening summer droughts which would render an adaptation of this kind of great survival value. Of the more conservative or typical grazing camels with relatively short limbs and sub-hypsodont grinders the characteristic forms are *Miolabis*, which succeeds the Lower Mio-

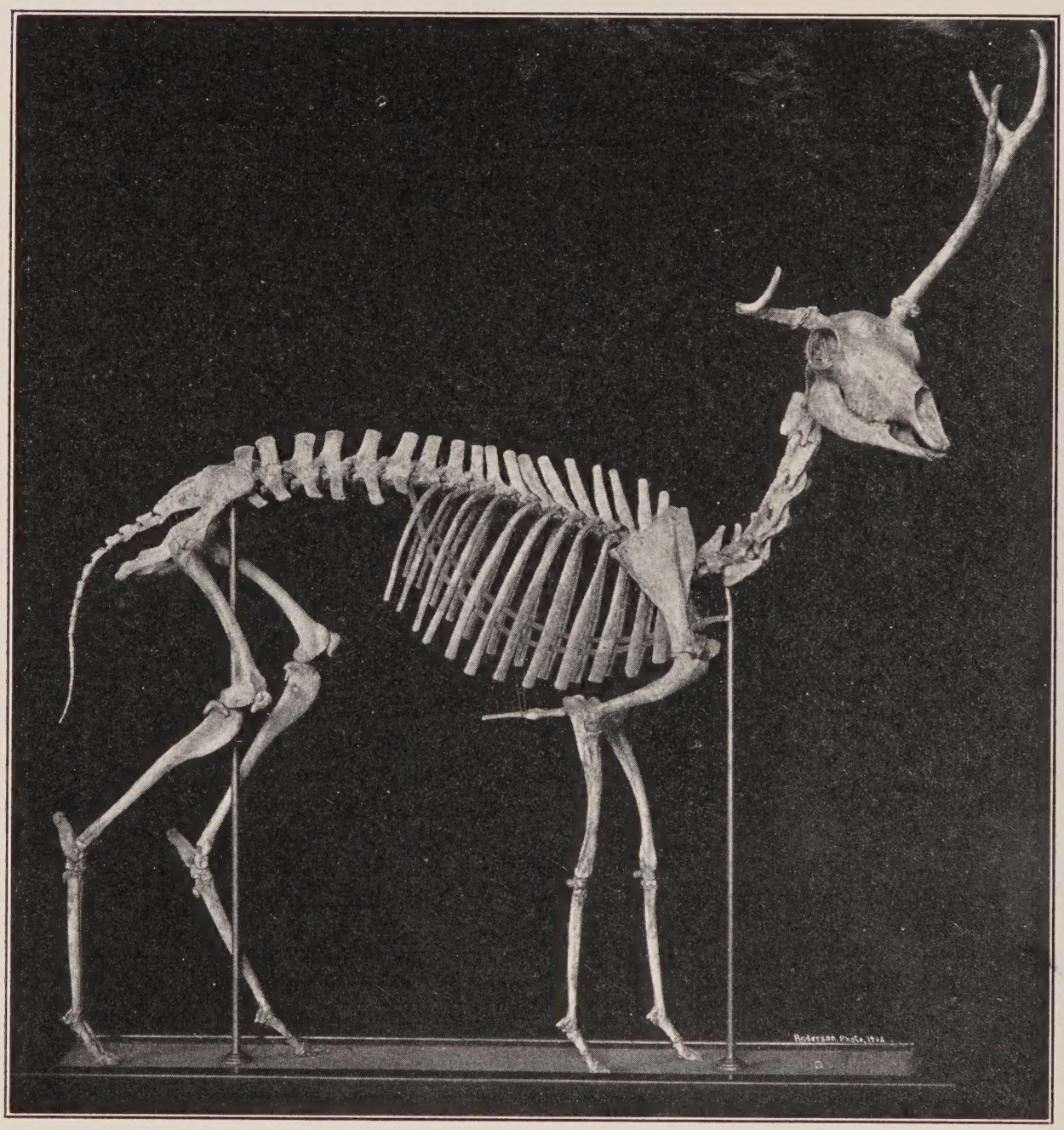


FIG. 146. — Skeleton of the deer-antelope *Merycodus osborni*. In the American Museum of Natural History. After Matthew.

cene *Protomeryx*, and *Protolabis*, which includes certain long-headed forms, readily distinguished from its successor *Procamelus* by the presence of a full set of upper incisor teeth and by its separate or 'split' metapodials.

The presence of numerous small-horned and hornless, grazing and browsing ruminants lends an entirely new aspect to the plains and forest-border

fauna. These animals are of three different kinds. The first, *Merycodus*,[1] presented externally the appearance of a diminutive American deer, twenty inches high at the withers, with three-tined antlers nine inches in length. It is the leader of the newly appearing family of merycodonts, distinguished by the possession of the deciduous branching antlers of the American deer type combined with the skeletal characters of the American prong-horned antelopes (Antilocapridæ), and provided with elongate or hypsodont grinding

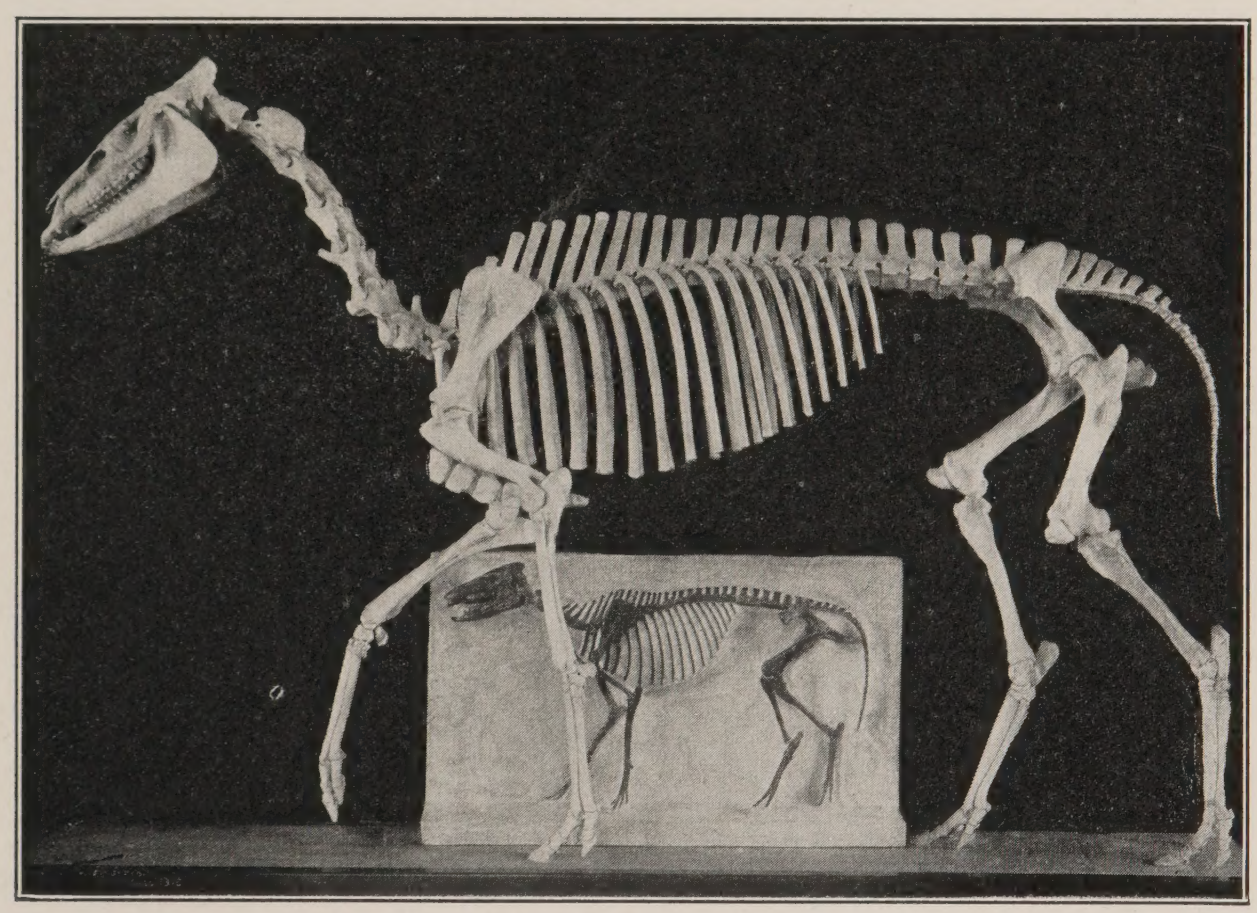


FIG. 147. — Skeletons of the Eocene four-toed horse *Eohippus venticolus*, and of the Miocene forest or browsing horse *Hypohippus osborni*. In the American Museum of Natural History.

teeth, thus a plains-living or grazing form. The second cervid type is a hornless animal of smaller proportions, known as *Blastomeryx*, a successor of *Leptomeryx*, and apparently a member of the American branch of the true Cervidæ. This is a browsing animal with short-crowned teeth; in its proportions it is similar to the cervuline or musk deer of Europe; it stands twelve to eighteen inches high at the shoulders, and is hornless.[2] The third ruminant of this stage is *Dromomeryx*, also a brachyodont or browsing form, of larger size, closely similar in its tooth structure to the hornless *Palæomeryx*

[1] See Matthew, W. D., A Complete Skeleton of *Merycodus*. *Bull. Amer. Mus. Nat. Hist.*, Vol. XX, 1904, p. 128.

In the Antilocapridæ the bony horn core is permanent like that of the Bovinæ, but the horn sheath is annually shed, a very peculiar combination of characters.

[2] The beginnings of antlers appear only in the Upper Miocene representatives of this phylum (Scott).

of Europe, but actually related to the cavicorn antelopine or bovid division of the Ruminantia. Species of *Dromomeryx* from Colorado (*D. borealis*) belong to an animal of the size of the existing Virginia deer. The horn pedicles are without 'burr,' apparently not deciduous and probably enclosed in a horny sheath as in the true antelopes and cattle.

There is a great variety of canids both of the long- and short-faced types. The abundance of these animals in the Miocene of North America, contrasted

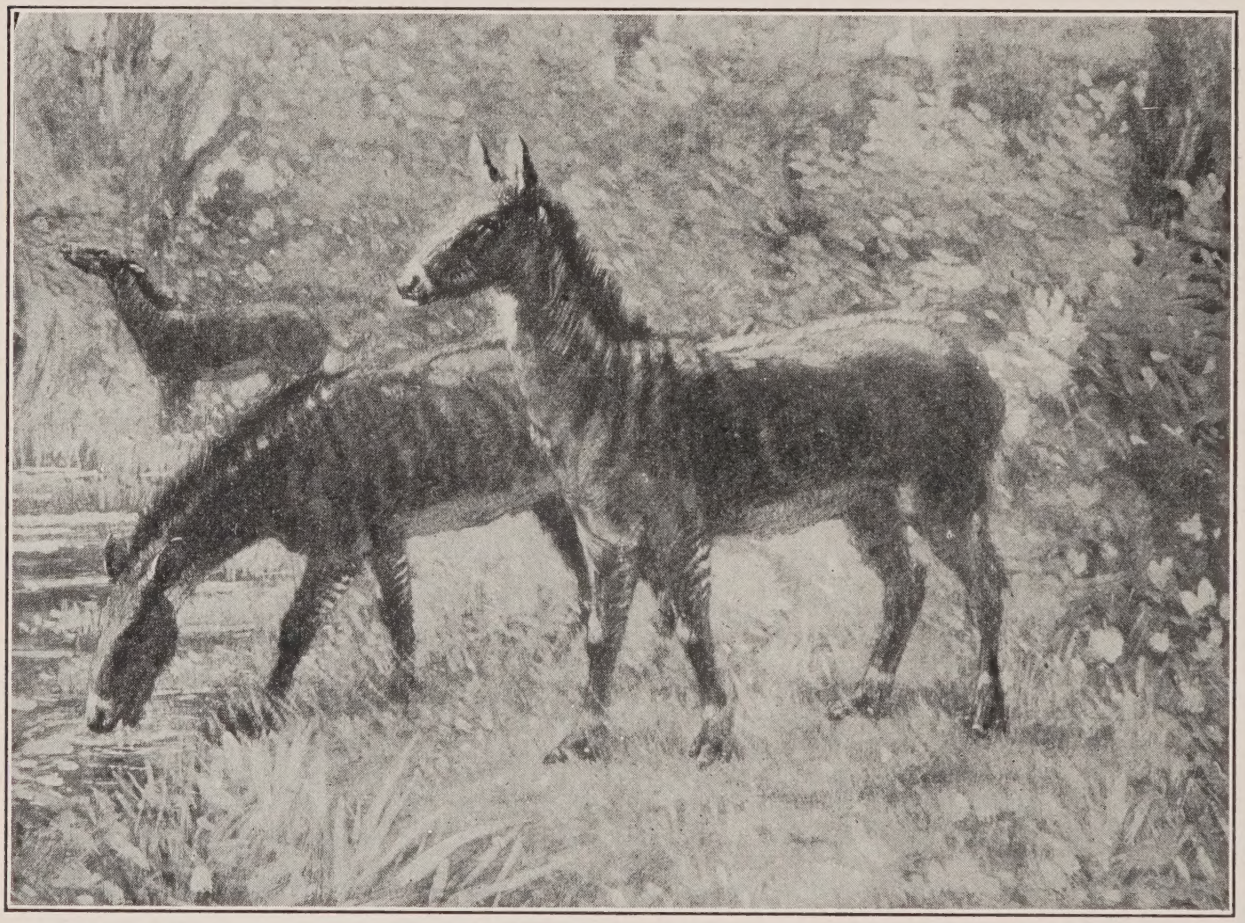


FIG. 148. — The Upper Miocene forest-living or browsing horse *Hypohippus*. After original by Charles R. Knight in the American Museum of Natural History.

with their subordinate position in Europe, renders it very probable that this continent was the chief center of their adaptive radiation. As studied by Scott, Matthew, and Merriam, they are in a high degree polyphyletic, including five or six distinct lines, as follows: The typical dogs, descendants of *Cynodictis* of the Oligocene, are represented by *Tephrocyon* and lead in the direction of *Canis*. The cyons or dhole-like dogs are successors to the *Temnocyon* and *Daphœnus* of the Oligocene with trenchant-heeled grinding teeth, and are represented by *Cyon* and *Icticyon*. The giant or bear-like dogs are represented by *Amphicyon*. The mustelid family is represented by a species of marten, by a primitive otter, as above noted, while the felids of Colorado are represented only by specimens doubtfully referred to the European *Pseudælurus*. It is noteworthy that none of the machærodonts have been discovered at this stage, although they are abundant both in older and in more recent formations.

Most remarkable of all the rodents are the short-headed mylagaulids, which may be regarded, together with the sewellels or haplodontids and Eocene and Oligocene ischyromyids, as a primitive division of the sciuromorph rodents. Beside the typical genus *Mylagaulus*, there has been discovered the extraordinary *Ceratogaulus rhinocerus*, which has a special horn-bearing bone on the nasals, which was undoubtedly capped with a prominent pointed dermal horn.

Upper Miocene

Hipparion and Procamelus Zone

The appearance in great numbers of herbivores with long-crowned or grazing teeth such as the horses (*Protohippus* and *Hipparion*) and the camels (*Procamelus*) establishes at once a broad evolution parallel with the Upper Miocene of Pikermi, of Eppelsheim, and of Mont Léberon. The teeth and feet of these animals demonstrate beyond question the spread in America as in Europe at the close of the Miocene of great, dry, grassy plains, of droughts or arid seasons, of long distances between the water pools at certain seasons of the year; in short, of East African and plateau conditions of life.

While no new mammals especially distinctive of western Europe appear in America at this time, it is evident that in *Protohippus* and *Hipparion* there was an invasion of progressive types from the north, either from British Columbia or from northern Asia. It is a striking fact that while *Protohippus* and *Hipparion* may have been descended from certain stages of the highly characteristic Middle Miocene *Merychippus*, horses of the genus *Merychippus* as well as of the primitive *Parahippus* and of the forest horse *Hypohippus* still persist in the Upper Miocene side by side with the highly specialized and hypsodont *Protohippus* and *Hipparion*. This is in wide contrast with the Old World, in which only the *Hipparion* type is known. Browsing horses (*Hypohippus*) occur with the hipparions in China.

This Upper Miocene fauna was very widespread geographically, very rich in specific forms, highly varied in character, and represented by numbers of complete skeletons. In other words, the American, like the European Miocene, closes with a great and famous mammalian fauna.

Geologic formations. Plains region. — This is the typical 'Loup Fork' of all the early literature of Hayden, Leidy, Marsh, Cope, also of Scott and Osborn in part. But the deposits to which the names 'Loup Fork' and 'Loup River' were originally applied lie in eastern Nebraska and are of Upper Pliocene or Lower Pleistocene age; the term Loup Fork was also stretched to cover Middle Miocene formations, and gradually lost all definite meaning. Typical Upper Miocene deposits of western Nebraska were named the 'Nebraska Formation' by Scott in 1894;[1] officially, however,

[1] Scott, *Bull. Geol. Soc. Amer.*, Vol. V, 1894, p. 595.

'Nebraska' is preoccupied, and by the U.S. Geological Survey this formation is known as the '*Ogallala*' of Darton. It consists of widely scattered river channel and flood plain deposits in South Dakota and Nebraska. To the south in New Mexico are the Santa Fe Marls, determined as of this age by Cope in 1884. In northwestern Texas are the Clarendon beds of Gidley, a river channel deposit overlying the Panhandle, Middle Miocene, at the edge of the Llano Estacado (Fig. 167). On the northern plains of Montana are the Madison Valley beds of Douglass, 1,200 feet in thickness.

From Montana on the northwest to Texas on the southwest, to Nebraska and Kansas in the central west, we find a very similar list of mammals, so that the homotaxis of the American horizons 'Nebraska,' 'Ogallala,' 'Clarendon,' 'Santa Fe,' 'Madison Valley,' and numerous others unnamed is singularly well established. They may be said to belong to the Hipparion Zone, a term equivalent to the Procamelus Zone of Cope, the Cosoryx Zone of Scott (1894), the Protohippus Zone of Osborn (1907).

The climatic conditions and flora of the high mountain region at about this time are well pictured in the description of the Florissant Lake of Colorado given on p. 283. There is evidence of occasional dust burials by a wind or sand storm in the discovery of remains of six hipparions on Little White River near the Rosebud Agency in South Dakota.[1] This discovery included the perfect skeleton of a female, the type of *Neohipparion whitneyi*, found closely crowded against those of several younger horses of the same species, the group having perished together either in a sand storm or by a stroke of lightning; the association of the younger horses with the mare is a natural one, indicating that this group had not been brought together by stream action. In the original description of the superb type specimen (Fig. 123) of this group Gidley pointed out that its limbs had the delicate proportions of those of the Virginia deer. With its strongly hypsodont and long-crowned teeth it represents a typical horse of the arid country.

The conspectus of this Upper Miocene fauna shows it as of prevailing American type.

PREVAILING MAMMALS

Proboscidea
Trilophodon
Rhinoceroses
Teleoceras, Aphelops
Tapirs
Tapiravus

As set forth in this summary there is a balance between the grazing and browsing types of Herbivora. Each great order of herbivores exhibits an increasingly sharp division between the more conservative browsing types with short-crowned teeth, and the more progressive grazing types with long-crowned teeth. Among the horses, the browsers (*Hypohippus* and *Parahippus*) are beginning to

[1] J. W. Gidley, A New Three-toed Horse. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX, July 24, 1903, p. 465.

PREVAILING MAMMALS

Horses
Hypohippus
Parahippus
Merychippus
Protohippus
Neohipparion
Peccaries
Prosthennops
Oreodonts
Pronomotherium
Merycochœrus
Camels
Procamelus
Pliauchenia
Deer
Blastomeryx
(horned)
Merycodonts
Cavicornia
Dromomeryx
Canids
Procyonids
Felids
Machærodonts

decline. The river-border and forest-living oreodonts are among the declining types soon to become extinct. The browsing tapirs are represented only by a single recorded specimen of *Tapiravus*. The true browsing or 'giraffe camels' (*Alticamelus*) so highly characteristic of the Lower and Middle Miocene have not thus far been discovered at all in the Upper Miocene, although we are certain that these animals were not yet extinct, because remains of them are again found in the Lower Pliocene Rattlesnake Formation of Oregon. Grazing camels with hypsodont teeth (*Procamelus* and *Pliauchenia*) are very abundant and specifically varied. The more primitive hypsodont camel known as *Protolabis* still survived in Montana. The wide geographic range of these camels in North America is most remarkable. They were certainly present in great herds, and lent the most characteristic aspect to the landscape. Soon after this period they are first recorded in Asia in the Siwaliks of the sub-Himalayas. Among the ruminants, the brachyodont browsing *Dromomeryx* and *Blastomeryx* still survive and are highly characteristic. At this time *Blastomeryx* first appears with horns. Certain of the rhinoceroses are also of the browsing type, and all the new mastodons must be placed in this category. It is noteworthy that the browsing chalicotheres, represented by the giant *Ancylotherium* of the Upper Miocene of Europe, have not yet been discovered in North America. The grazing animals are on the whole more numerous, more varied, and more characteristic.

A very typical proboscidean is the *Trilophodon productus*, a doubtful specimen of which was discovered by Gidley in the Clarendon Formation of Texas. The skull of this mastodon is broad

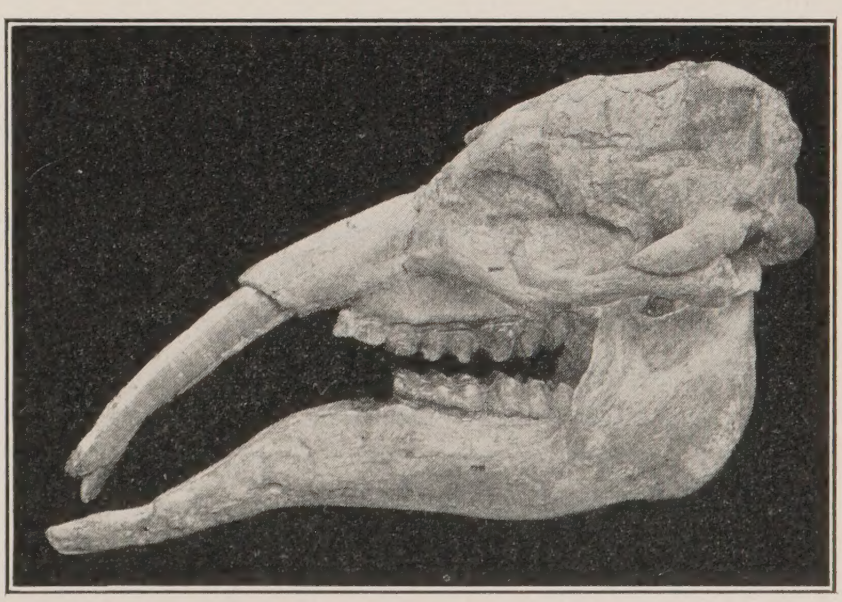


FIG. 149. — Skull of the primitive four-tusked mastodon, *Trilophodon productus*, of the Upper Miocene of Texas. In the American Museum of Natural History.

and flat; the upper tusks are directed downward and outward, and ornamented with a ribbon-like band of enamel; the lower tusks still retain the horizontally flattened form characteristic of *Palæomastodon*, and the degree of attrition indicates that they were in constant use in feeding. The lower jaws are still elongate. From the parts of a skeleton attributed to one of these animals, we may estimate the height as 5 ft. 10 in. at the withers. The trilophodont molars indicate that this animal may have been in the same line of descent as the great *Mastodon americanus* of the Pleistocene.

The teleocerine rhinoceroses at this stage are represented by the species *T. crassus*, which is somewhat less hypsodont than the *T. fossiger* of the next stage. Similarly the aceratheres (*Aphelops brachyodus*) have not yet attained the final stage of evolution. Two of these animals from the Flint Creek beds of Montana[1] (*A. montanus*, *A. ceratorhinus*) exhibit dolichocephalic skulls, long and slender nasals, sometimes with small terminal horn rugosities (*A. ceratorhinus*), brachyodont teeth, limbs relatively long and slender. These proportions are in wide contrast with those of the broad-skulled, short-footed contemporary *Teleoceras* of Montana, which exhibits short nasals with a small laterally compressed terminal horn (*?T. crassus*).

The tapirs were very rare.

The horses present a very high degree of adaptive radiation, fitted to the diversified feeding grounds of the plains region and to the forests and thickets bordering the streams. All of these horses exhibit pits or depressions on the side of the face in front of the eyes, a character which points away from rather than toward the ancestors of *Equus*.

The oreodonts include the persistent Miocene genera *Merychyus* and *Merycochœrus*, and in the Madison Valley beds of Montana there appears the remarkable *Pronomotherium*, an extremely specialized brachycephalic oreodont, with receding nasals, indicating in the plainest manner the possession of a large proboscis.[2] Even in *Merycochœrus* the face is greatly shortened and probably supplied with a flexible upper lip and much shorter jaw than the Upper Oligocene *Promerycochœrus*. The abbreviation of the skull and adoption of fluviatile habits appear to have been features of the closing chapter of the oreodont evolution.

Among the camels *Procamelus* is readily distinguished from the Middle Miocene *Protolabis* by the loss of two upper incisor teeth, a marked approach to *Camelus*. The contemporary *Pliauchenia* is distinguished by the loss of some of its premolar teeth, thus approaching the llamas, or South American camels (*Auchenia*), in which the premolars are more reduced than in the

[1] Douglass, E., New Vertebrates from the Montana Tertiary. *Ann. Carneg. Mus., Pittsburg*, Vol. II, no. 2, 1903, pp. 145–200.

[2] Douglass, E., *Promerycochœrus* and a New Genus of Merycoidodonts with Some Notes on Other Agriochœridæ. *Ann. Carneg. Mus., Pittsburg*, Vol. IV, No. 2, 1907.

true camels. *Procamelus* is a highly varied form, including massive as well as more slender and graceful types, but the limbs are of moderate length, or proportioned as in the recent camels; it is regarded as a generalized form which may have given rise to both the New and Old World camels.

The ancient camels of Montana have been investigated recently by Douglass[1] and are shown to include two species (*Procamelus elrodi, P. madisonius*). The former contrasts widely in the proportions of its head and neck with the *Alticamelus altus* of Matthew, because the head is nearly as large, while the neck is very much shorter, the total length of the neck being 1,036 mm., while that of *A. altus* is 1,560 mm., or half as long again.

The American deer family is still represented by the genus *Blastomeryx* (*B. wellsi*). Scott has reported a horned member of this phylum. At this stage we first come to know, through the explorations of Douglass in Montana,[2] the true characters of the form which has long figured in palæontological literature as *Blastomeryx* and *Palæomeryx*, but was really an entirely distinct animal, to which Douglass has given the name *Dromomeryx*. There are some reasons for considering it not one of the Cervicornia, but one of the Cavicornia, resembling in certain characters the American prong-horned antelope, or *Antilocapra*, in others some of the Old World antelopes, although the teeth are still of the brachyodont or browsing type. Matthew, on the other hand, doubts whether it is distinct from the original deer-like *Palæomeryx*. Contemporary with these forms were several species of *Merycodus*, with its cervid antlers of the deciduous type. The peccaries are represented by *Prosthennops*.

Among the raptorial types the machærodonts reappear, animals of large size, accompanied by a form resembling the Miocene *Pseudælurus* of Europe, of the species *P. intrepidus*. Among the mustelids we find the marten (*Mustela*), weasel (*Putorius*), primitive otter (*Potamotherium*), and the first recorded appearance in America of the true otter (*Lutra*). These animals are fairly abundant in the river channel formations of this period. Similarly the raccoon or procyonid family is represented by a form (*Leptarctus*) more modern in type than the Middle Miocene *Phlaocyon;* Wortman[3] observed (p. 239), "This animal offers a number of transitional characters between the more typical Procyonidæ and the aberrant *Cercoleptes*."

The canids include several species of *Ælurodon*, a typical dog derived from the *Tephrocyon* type of the Middle Miocene. Another canid (*Ischyrocyon*) is intermediate between the *Cyon* or dhole and the *Amphicyon* group, with large grinding teeth as in the latter. It is interesting to note that the

[1] Douglass, E., A Description of a New Species of *Procamelus* from the Upper Miocene of Montana with Notes upon *Procamelus madisonius* Douglass. *Ann. Carneg. Mus.*, Vol. V, nos. 2 and 3, 1909, pp. 159–165.

[2] Douglass, E., *Dromomeryx*, a New Genus of American Ruminants. *Ann. Carneg. Mus.* Vol. V, no. 11, 1908–1909, pp. 457–479.

[3] See Wortman, J. L., On the Affinities of *Leptarctus primus*. *Bull. Amer. Mus. Nat. Hist.*, Vol. VI, 1894.

first amphicyon-like animal recognized in America is the species *A. americanus*, described by Wortman [1] in 1901, one of a number of somewhat atypical forms to which Cope gave the name *Borophagus*, animals differing from the typical amphicyons of Europe. As in the Old World, these are truly the giant carnivores of the period, some of them rivaling the largest existing bears in size. Thus the *D. gidleyi* of the Clarendon beds of Texas has a head as large as that of the great brown or Kadiak bear of Alaska. The rodents of this period include squirrels, marmots, and mylagaulids, gophers, murids, leporids, and castorids. Among the last is the species *Eucastor* (*Dipoides tortus*), which presents a resemblance to the giant *Castoroïdes* of the Pleistocene.[2]

Miocene History of American Deer

All the New World or American deer (*Odocoileus, Mazama*, etc.) are known to stand well apart from the Old World deer (*Cervus*) in two important characters, namely, the absence of the brow tine of the antler and in the preservation of the distal portion of the lateral metacarpals. They are thus termed *telemetacarpal*, while *Cervus* is termed *plesiometacarpal* because the proximal portion of the metacarpals is preserved. It appears certain that the *Odocoileus* and *Cervus* phyla have been separated since very ancient times. According to the observations of Matthew [3] the diminutive *Leptomeryx* of the American Lower Oligocene is an extremely unspecialized ruminant related to the primitive American cervids. It is possible that through the Miocene *Blastomeryx* it may be a direct ancestor of the deer; *Blastomeryx* is analogous to the Miocene deer of the Old World, being armed with powerful canine tusks in the Lower Miocene stage (*B. primus*), and not acquiring horns, 'antlers,' until Upper Miocene times (*B. antilopinus* Scott, *B. borealis* Cope). The *Dromomeryx* of Douglass is also to be considered in this connection. The Pliocene stage of the browsing American deer with simple antlers has not yet been discovered; it should be somewhat more primitive than the North American *Odocoileus* and resemble rather the South American deer (*Mazama*) which occurs in Pleistocene and recent times in that country.

[1] Wortman, *Amer. Jour. Sci.*, 1901.

[2] Matthew, W. D., A Horned Rodent from the Colorado Miocene. With a Revision of the Mylagauli, Beavers, and Hares of the American Tertiary. *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI, Art. xxii, 1902, p. 304.

[3] Matthew, W. D., Osteology of *Blastomeryx* and Phylogeny of the American Cervidæ. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, Art. xxvii, June 30, 1908, pp. 535–562. Speaking more fully, Dr. Matthew's theory is that there was a common North Asiatic *center of evolution* which contributed to Europe and North America, respectively, various stages in the evolution of the deer.

CHAPTER V

THE PLIOCENE OF EUROPE, ASIA, AND NORTH AMERICA

The Pliocene life of Europe and Asia is relatively well known, while that of North America is imperfectly known; therefore only the broadest time parallels can be drawn. The extension of our knowledge to the mammals of India, China, and North Africa is full of interest and importance.

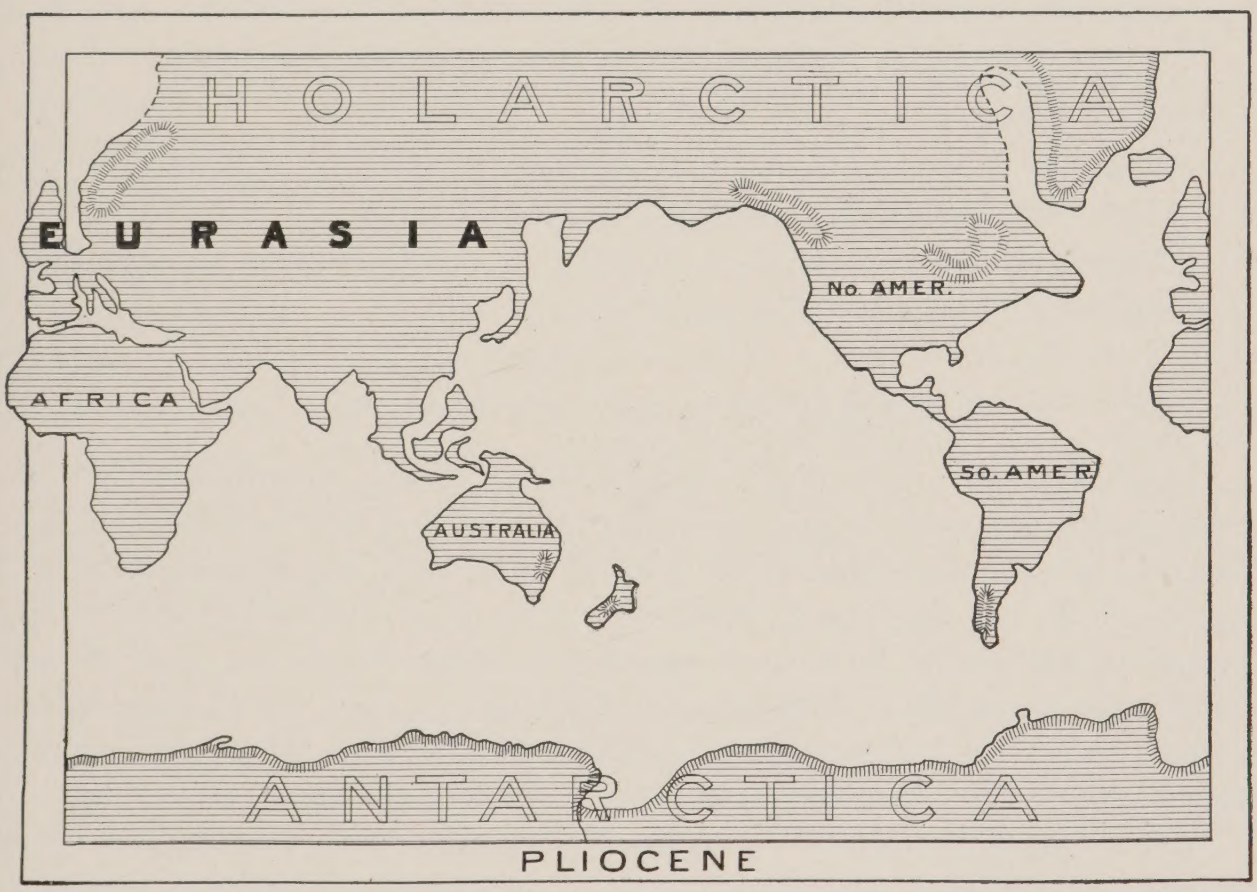


Fig. 150. — **Middle and Upper Pliocene.** A period of continued continental elevation, especially in Europe and Eastern North America. Seasons of aridity or summer drought, increased aridity of the Great Plains of North America. South America connected with North America by migration routes which allowed free interchange of mammals. Australia still united with New Guinea and Tasmania. Rearranged after W. D. Matthew, 1908.

In course of the Pliocene we enter upon the sixth grand faunal phase (p. 304), which can only be understood through a preliminary survey of the general changes and prevailing mammalian life in each of the northern continents.

The geographic conditions in Africa, Europe, Asia, and North America favored the wide dispersal of similar forms of mammals, which reached a

climax in the temporary unification into one grand zoölogical region of all the great continents, excepting Australia. This somewhat extreme statement may be made for the sake of emphasis, but it is well within the bounds of truth to say that never before or since in geologic time has the mammalian life of the globe enjoyed such a widespread and uniform distribution as during closing Miocene and Pliocene times.

VI. SIXTH FAUNAL PHASE. — PLIOCENE TO MIDDLE PLEISTOCENE MODERNIZATION. INTERCHANGE AND WIDE DISTRIBUTION OF CERTAIN MIGRATING MAMMALS IN AFRICA, EURASIA, AND NORTH AMERICA. SECOND ENTRANCE INTO NORTH AMERICA OF SOUTH AMERICAN MAMMALS. INVASION OF SOUTH AMERICA BY MAMMALS OF NORTH AMERICAN, ASIATIC, EUROPEAN, AND AFRICAN ORIGIN. CONTINUED INDEPENDENT EVOLUTION OF NON-MIGRATING MAMMALS IN THE NEW AND OLD WORLDS. GRADUAL ADVANCE OF MORE TEMPERATE CLIMATIC CONDITIONS IN THE NORTHERN HEMISPHERE AND INVASION OF NEW FOREST OR BROWSING TYPES FROM THE NORTH.

I. PLIOCENE LIFE OF EUROPE

Modernization. — The final modernization of the mammalian life of southern Europe may be said to have commenced at the beginning of the Pliocene, to have continued in the gradual withdrawal of plateau and desert types and in the appearance from the north of new browsing forest and aquatic types, and to have been completed during the glacial stage of the Pleistocene. Contemporaneously with these life changes, the physiography, climate, and flora also gradually assumed their present or modern condition, but only after the great fluctuations of the Pleistocene, or Ice Age.

While the mammals of the early Pliocene are little known, the very opening of the epoch is defined by many *disappearances* caused both by *emigration* and *extinction*, whereby Europe lost much of its prevailing south-Asiatic and Ethiopian aspect. The chief animals which had left the country are the giraffes, most of the Asiatic or African antelopes, the two-horned African rhinoceroses, the aardvarks, and the anthropoid apes allied to the gibbon and chimpanzee. There remained only two types of antelopes allied to *Oryx* and to the gazelle, and the hipparions, which may have resembled the zebras in external appearance.

Palæogeography. — The Pliocene epoch opened with a reversal of the conditions of the Upper Miocene, namely, a contraction of the vast land areas or grazing plateaux of southern Europe, which had been so favorable

to the Asiatic-African period of the mammalian life of Pikermi and Mt. Léberon. The entire geographic history of the epoch extends from the time of the completion of the Swiss Alps to the establishment of the main coast lines of Europe, the last touches being given to these lines in the late Pleistocene and contributing their modern aspects. The Pliocene was marked throughout by continuous volcanic disturbances. The extinctions and disappearances of mammals are in themselves proof of very profound physiographic changes between the close of the Miocene and the first mammaliferous records of the Lower Pliocene, namely, of *depression* as contrasted with the extreme *elevation* at the close of the Miocene.

At the beginning of the epoch, or Plaisancian stage, the Straits of Gibraltar were formed, and communication between the Atlantic and Mediterranean was reëstablished. A bay extended into the valley of the Rhone; Italy was submerged except for the Apennines and a part of Sicily.[1]

The Middle Pliocene, or Astian, named from the region of Asti in Piedmont, is also a stage of marine depression which surrounds almost the entire Mediterranean basin, representing in importance as well as in duration the greater part of the Pliocene. The fauna denotes a rather warm sea. Toward the close of the Middle Pliocene the reëlevation of the land and retreat of the sea left Italy with practically its present contours.

Consequently the Upper Pliocene of Italy is represented solely by freshwater deposits. It is the contemporaneous marine formations of Sicily, however, which give the name 'Sicilian' to this final Pliocene stage. The peninsula which connected the Balearic Islands, Corsica, and Sardinia with the mainland opened the Mediterranean more largely toward the east. Beyond the Ægean Sea there stretched the great open marine area of the Caspian and Baltic seas.

Stages	*Formations*	*Characteristic Faunas*
3. *Sicilian* Elevation and modern coast lines.	A marine phase in Sicily. Freshwater fluvio-lacustrine deposits of northern Italy and Central France.	Fauna of the upper Val d'Arno and of Olivola in Tuscany; of Perrier and Coupet in central France.
2. *Astian* Closing with elevation.	Marine deposits in northern Italy (Asti). Freshwater deposits of southern France.	Fauna of southern France, Roussillon, of Montpellier (Hérault); flora of Meximieux (Saône valley).
1. *Plaisancian* Maximum depression.	Depression and marine deposition in northern Italy (Plaisantin), deep depression of the Po and Rhone valleys of southern France.	Lignites of Casino (Tuscany); Autrey in Saône valley.

[1] De Lapparent, A., Traité de Géologie, 1906, p. 1633.

Flora and climate. — Owing to the expansion of the warm Mediterranean Sea, the climate of the Lower Pliocene is mild. The very gradual cooling or lowering of temperature continues. The entire Pliocene epoch was marked by the slow southward advance of the northern forest types of trees and by the corresponding recession to the south of the more delicate types, the palms, for example, being driven 10° farther south.[1] The European flora gradually loses its large palms and camphor trees; the sabal (*Sabal*) flourishes for a while in Languedoc, and the dwarf fan palm (*Chamærops*) maintains its existence near Marseilles up to the end of the Pliocene period. After having retained for so long a time the sequoias (*Sequoia*) and bamboos (*Bambusa*), Europe becomes populated with species very similar to those of its present tree flora.

A marked and most interesting peculiarity is that several very characteristic Pliocene species of Europe are now found only in the great forests of North America.[2] Thus in the Pliocene of Europe there occur such trees as the locust (*Robinia*), the honey locust (*Gleditschia*), the sumac (*Rhus*), the bald cypress (*Taxodium*), the tulip tree (*Liriodendron*), the sweet gum (*Liquidambar*), the sour gum (*Nissa*), which do not now occur in Europe, but are at present very characteristic forms of the flora of temperate North America.[3] The oak (*Quercus*), beech (*Fagus*), maple (*Acer*), poplar (*Populus*), walnut (*Juglans*), and the larch (*Larix*) predominate in central France, and include forms which show affinities to existing types of North Africa (Algeria), southern Europe (Portugal), and even Japan. Toward the very end of the Pliocene there is a marked lowering of temperature, and in the higher mountainous areas there was perhaps a beginning of glacial stages.

Other authorities[4] believe that in the Pliocene there occurred a still greater fall of temperature, that while we cannot speak of a uniform climate over all Europe during the Miocene, this is even less the case during the Pliocene. The flora undergoes a corresponding change, and there appear many forms which seem to be identical with modern types, or at least are varieties of recent species.

Against the gradual cooling theory, however, may be cited the opinion expressed by Depéret in 1893[5] that the Pliocene flora shows great uniformity throughout, even in deposits of quite different ages; that from beginning to end, the Pliocene flora of southern France and Italy shows none but the slightest changes. This opinion is based upon the fact that the deposits of the Val d'Arno, northern Italy, represent the entire range of the Pliocene,

[1] Depéret, C., Note sur la Succession stratigraphique des Faunes de Mammifères Pliocènes de l'Europe et du Plateau Central en particulier. *Bull. Soc. Géol. France*, Ser. 3, Vol. XXI, 1893, p. 529.

[2] De Lapparent, A., Traité de Géologie, 1906, p. 1635.

[3] Nicholson, H. A., A Manual of Palæontology, Edinburgh and London, 1879, Vol. II, p. 476.

[4] Schimper und Schenk, Palæophytologie, 1890, p. 821.

[5] Depéret, C., Note sur la Succession stratigraphique des Faunes de Mammifères Pliocènes de l'Europe, 1893, p. 528.

and yet the flora from the lower strata is indistinguishable from that of the upper.[1] In the Val d'Arno we find the sassafras, bay, laurel, magnolia, sweet gum, etc.; thus the regions which harbored the rich forest and meadow fauna of northern Italy in Upper Pliocene times abounded in trees familiar to-day in the Carolinas of the southern United States. Similarly the famous flora of Meximieux is regarded by Depéret as representing all the levels of the Pliocene. At Meximieux the bamboo (*Bambusa*) is characteristic.

Pliocene birds. — The fossils preserved in the numerous marine and littoral formations of the Pliocene give us a picture of the substantially modern character of the shore bird life of Europe, which may be compared with that of North America, p. 459. In the Lower Pliocene of England we discover in the Red Crag of Suffolk remains of *Diomedea*, an albatross slightly smaller than the existing 'frigate birds' (*Fregata*). In northern Italy are found the coot (*Fulica*), guillemots (*Uria*) of the size of the recent spectacled guillemot, and the falcons (*Falco*). In the Middle Pliocene of Montpellier and Roussillon we find representatives of the existing Grallæ (including herons, etc.) and of the family of Anatidæ (which comprises the ducks and swans), as well as gallinaceous forms (*Gallus*) related to Indo-Malayan types. There were also crows (*Corvus*) and thrushes (*Turdus*) similar to existing European forms.[2]

Pliocene primates.[3] — In the Pliocene appear three of the catarrhine monkeys closely related to the still living langur (*Semnopithecus*), to the macaque (*Macacus*), and to the baboon (*Cynocephalus*). The *Dolichopithecus* of France (Perpignan) is distinguished from the existing langur of southern Asia through its elongate face and its relatively short and stout limbs.

The anthropoid apes do not survive in Europe; *Dryopithecus* appears to have become extinct, as well as the gibbon line, which we have seen represented in the *Pliohylobates* of the Upper Miocene of Eppelsheim.

The chimpanzee from the Pliocene of the Siwalik Hills, commonly designated as *Palæopithecus sivalensis*, is fully identified by Schlosser with the existing chimpanzee (*Anthropopithecus*). According to Schlosser, also, there is positive evidence of the existence of the orang (*Simia*) in the Siwaliks, but fossil remains of the gorilla (*Gorilla*) have not yet been discovered.

To be reckoned with the primates also are the undiscovered makers of the eoliths, or primitive flints found in various parts of Europe.

[1] Ristori, Contrib. alla flora foss. d. Val d'Arno sup. *Atti Soc. Toscana Sc.*, Vol. VII, 1886; also Consid. geol. s. Val d'Arno, *id.* p. 256 seq.

[2] Depéret, C., Les Animaux Pliocènes du Roussillon. *Mem. Soc. Géol. France*, Paléont., no. 3, Paris, 1890, pp. 127–138.

[3] Schwalbe, G., Über fossile Primaten und ihre Bedeutung für die Vorgeschichte des Menschen. *Mitteil. Philomat. Ges. Elsass-Lothringen*, Vol. IV, no. 1, Decade 16 (1908), Strassburg, 1909, pp. 45–61.

PARTIAL LIST OF PLIOCENE MAMMALS OF THE NEW AND OLD WORLDS

Peculiar to Europe and Asia	*Common to Europe, Asia, and North America*	*Peculiar to North America*
I. Lower and Middle Pliocene	I. Lower and Middle Pliocene	I. Lower and Middle Pliocene
Roe deer (*Capreolus*)	Mastodons (tetralophodont and trilophodont)	Last oreodonts
True antelopes and gazelles	Last hornless and teleocerine rhinoceroses (not in Europe)	Camels and llamas
Sumatran rhinoceroses (*Dicerorhinus*)	Hipparions	Ancestral horses
True rhinoceroses (*Rhinoceros*, Asia only)	Bovid antelopes	Ancestral American deer
African and Asiatic monkeys	Tapirs [1]	Merycodonts
True boars (*Sus*)	Mustelids	Dicotylids or peccaries
Porcupines (*Hystrix*)	Canids	Haplodonts, sewellels
Tailless hares (*Lagomys*)	Machærodonts	Geomyids, gophers
Hyænas (*Hyæna*)	Felids (*Felis*)	Procyonids
Dog-bears (*Hyænarctos*)	Murids [1] (*Mus*)	Amphicyonids, or giant dogs
Civets (*Viverra*)	Hares [1] (*Lepus*)	Gravigrade edentates (Megalonychids)
Bears (*Ursus*)	Otters [1] (*Lutra*)	
Pandas (*Ailurus*)		
Wild Cat (*Felis catus*)		
Lynxes (*Felis lynx*)		
Foxes (*Vulpes*)		
II. Upper Pliocene	II. Upper Pliocene	II. Middle Pliocene of South American Origin
Polycladine and axis deer	Elephants (*Elephas*)	Glyptodont edentates
Bovines (*Bos*)	True horses (*Equus*)	Gravigrade edentates
Hippopotami	Camels (N. America, Asia)	
Macaques (*Macacus*)		
Voles (*Arvicola*)		
African murids (*Lophiomys*, *Ruscinomys*)		
Hamsters (*Cricetus*)		
Moles (*Talpa*)		
Shrews (*Sorex*, *Crocidura*)		

[1] These mammals undoubtedly existed in the American Pliocene, although they have not yet been recorded.

Faunal break with the Miocene. — The profound influences of the great earth movements of southern Europe on all the conditions of life are reflected in the faunal break between the Upper Miocene (Pikermi stage) and the Lower Pliocene (Plaisancian stage). As noted on p. 271, the advent of a new period is first negatively indicated by the *absence* in Europe of many carnivores, especially of the giant dogs (*Dinocyon*), of the short-faced dogs (*Simocyon*), of *Promephitis*, of the hyæna-like *Ictitherium* and *Hyænictis*, and of the anthropoid apes (gibbons). Among the herbivorous mammals no successors in Europe are found to the dinotheres (*Dinotherium*), chalicotheres (*Ancylotherium*), hornless rhinoceroses (*Aceratherium*), teleocerine rhinoceroses (*Teleoceras*), or African rhinoceroses (*Diceros*). The rhinoceroses evidently found conditions unfavorable, for beside the expulsion of the hornless and teleocerine types, the African two-horned types (*Diceros* or *Atelodus*), which were so abundant in the Upper Miocene, apparently migrated out of Europe, though destined to reappear again in the late Pleistocene. Thus the only rhinoceroses which have been discovered in Europe during the Pliocene belong to the two-horned, long-headed, ceratorhine, or Sumatran type (*Dicerorhinus*), and these are distinguished from the African two-horned types by the presence of anterior cutting teeth.

Faunal Divisions

As we have seen (p. 305), the natural divisions of the Pliocene are based upon *three* great marine stages, while the mammalian life is divided into *two* grand phases, as follows:

	Stages	*Fauna*	*Europe*	*North America*
Pliocene	Upper: Sicilian	The Newer Pliocene Fauna	New North and South Asiatic types. First *Elephas* and *Equus* Zone	Loup River Formation, *Elephas imperator* Zone
	Middle: Astian	The Older Pliocene Fauna	Surviving Miocene, African, and Asiatic types	Blanco Formation, *Hipparion* and *Glyptotherium* Zone
	Lower: Plaisancian	The Older Pliocene Fauna	Surviving Miocene, African, and Asiatic types	Republican River and Rattlesnake Formations, *Hipparion* and *Pliohippus* Zone

Thus, like the Miocene, the Pliocene of Europe has a grand and twofold division: it embraces an 'older fauna' of surviving resident types, and a 'newer fauna' of arriving types. Briefly, the *older fauna* is a con-

tinuation of part of the Upper Miocene fauna of Pontian age, followed by a gradual disappearance of many of these survivors.

The older Pliocene fauna.[1] — The older Pliocene fauna corresponds to the Lower (Plaisancian) and Middle (Astian) Pliocene stages. It is characterized by the persistence of the smaller number of Upper Miocene mammals;

FIG. 151. — **Pliocene.** Plaisancian. ENGLAND. — **1** *Coralline Crag* of Suffolk. FRANCE. — Minerai de fer d' **2** *Autrey* in the Saône Valley (région de la Bresse), lacustrine. ITALY. — Lignites of **3** *Casino* (Tuscany). Astian. ENGLAND. — **4** *Red Crag* of Suffolk, marine (large part). FRANCE. — Sables marins de **5** *Montpellier* (Hérault). Sables siliceux gris de **6** *Perpignan* in *Roussillon*, fluvio-lacustrine. Sables de **7** *Trévoux*, cailloutis de **8** *Montluel*, tufs de **9** *Meximieux*, in the Saône Valley (région de la Bresse). Sicilian. ENGLAND. — **10** *Norwich Crag* of Norfolk, fluvio-marine. FRANCE. — Sables et graviers de **11** *Chagny* in the Saône Valley. Graviers de **12** *Perrier*, fluviatile, *Ardé* (Puy-de-Dôme). **13** *Vialette*, *Coupet*, volcanic deposits, sables à mastodontes du *Puy*, *Sainzelles*, *la Malouteyre* (Haute-Loire). ITALY. — Marls and sands of **14** *Pareto* in northern Italy, fluvio-lacustrine. **15** *San Paolo* (Piedmont), **16** *Villafranca*, **17** *Ferrara*, **18** *Fossano* (Piedmont), in the Po Valley. **19** *Corniano*, **20** *Montopoli* near San Miniato, **21** *Empoli*, **22** *Siena*, in Tuscany. Ferruginous gravels of the **23** *Val d'Arno* ("Sansino beds," 60 meters), fluvio-lacustrine. **24** *Papigno*, lignites of **25** *Spoleto*, **26** *Assisi*, in Umbria. Lacustrine formations of **27** *Campagnano*, in Roma, **28** *Castelnuovo* in the Valley of the Serchio, **29** *Olivola*, in Province Massa Carrara (Tuscany). Correlation of Depéret.

the larger number of Upper Miocene mammals, as noted upon p. 271, have emigrated or become extinct. The persistent forms include the hipparions, a few large antelopes of African aspect (*Palæoryx cordieri*, *P. boödon*), large monkeys with Asiatic affinities, such as *Semnopithecus* and *Dolichopithecus*, allied to the langurs and macaques, rare anthropoid apes. Deer are in-

[1] Depéret, Succession stratigraphique des Faunes de Mammifères Pliocènes de l'Europe, 1893, p. 538.

frequent, and when present include only those with simple antlers like the roe deer (*Capreolus*). Among the rodents are two forms (*Trilophomys* and *Ruscinomys*) allied to the African crested rats. A flying squirrel (*Sciuropterus*) and a primitive beaver (*Chalicomys*) persist from the Miocene. Further details regarding this older fauna are given below in the description of the mammals of Roussillon. At Casino are recorded the newly arriving hippopotami (p. 313).

The *newer Pliocene fauna*[1] witnesses the disappearance of the last of the characteristic Miocene genera, among which only the mastodon survives until the close. The horse (*Equus stenonis*) replaces *Hipparion;* the Bovinæ appear in Europe for the first time (*Leptobos elatus*); monkeys continue in Italy, but are now represented by forms (*Macacus florentinus*) allied to the Barbary macaque of Gibraltar; the southern elephant (*Elephas meridionalis*) makes its appearance and coexists almost everywhere with *Mastodon arvernensis* and *M. borsoni.* This fauna has been found in various parts of Italy, France, and England. Not the least characteristic feature of this newer fauna is the abundance of large deer with elaborate antlers of the 'polycladine' type, as well as ancestors of the true *Cervus* or 'elaphine' type. The *newer fauna* of the Upper Pliocene is thus sharply defined by the expulsion or emigration of many of the resident Asiatic or African forms, and by the sudden introduction or appearance of several modern types which had probably evolved in North America, Asia, and possibly Africa, chief among which are the following animals:

Equus (*E. stenonis*) the true horses	North America
Leptobos (*L. elatus*) the first true cattle	Southern Asia
Cervus (*C. dicranius*), etc., polycladine deer	Northern Asia
Elephas (*E. meridionalis*) the true elephants	Asia or Africa

Summary. — Comparing this with the corresponding general history of Miocene life, p. 249, we observe that the Pliocene migrations and extinctions exactly reverse those of the Miocene.

The explanation of this interesting contrast is to be found in the reversed order of the physiographic changes in Europe, and of the changes in plant life, p. 244. In other words, while the Miocene closed with a period of warm, dry, open plains in southern Europe favorable to grazing or steppe types, the Pliocene closed with a moister period and the spread of forest and fluviatile conditions interspersed with meadows favorable to a great variety of browsing deer, as well as to the grazing elephants, horses, and cattle.

Lower Pliocene or Plaisancian

As this is chiefly a marine phase, the terrestrial mammalian fauna is imperfectly known. The typical deposits are those of the lignites of

[1] Depéret, Succession stratigraphique des Faunes de Mammifères Pliocènes de l'Europe. 1893, p. 539.

Casino (Tuscany) (Fig. 151, 3) which are correlated by Depéret[1] with the lacustrine deposits of Autrey (2) in the valley of the Saône, France. On the east coast of England is a marine formation, the Coralline Crag of Suffolk (1), containing mastodon and a rhinoceros (*Dicerorhinus*). This may

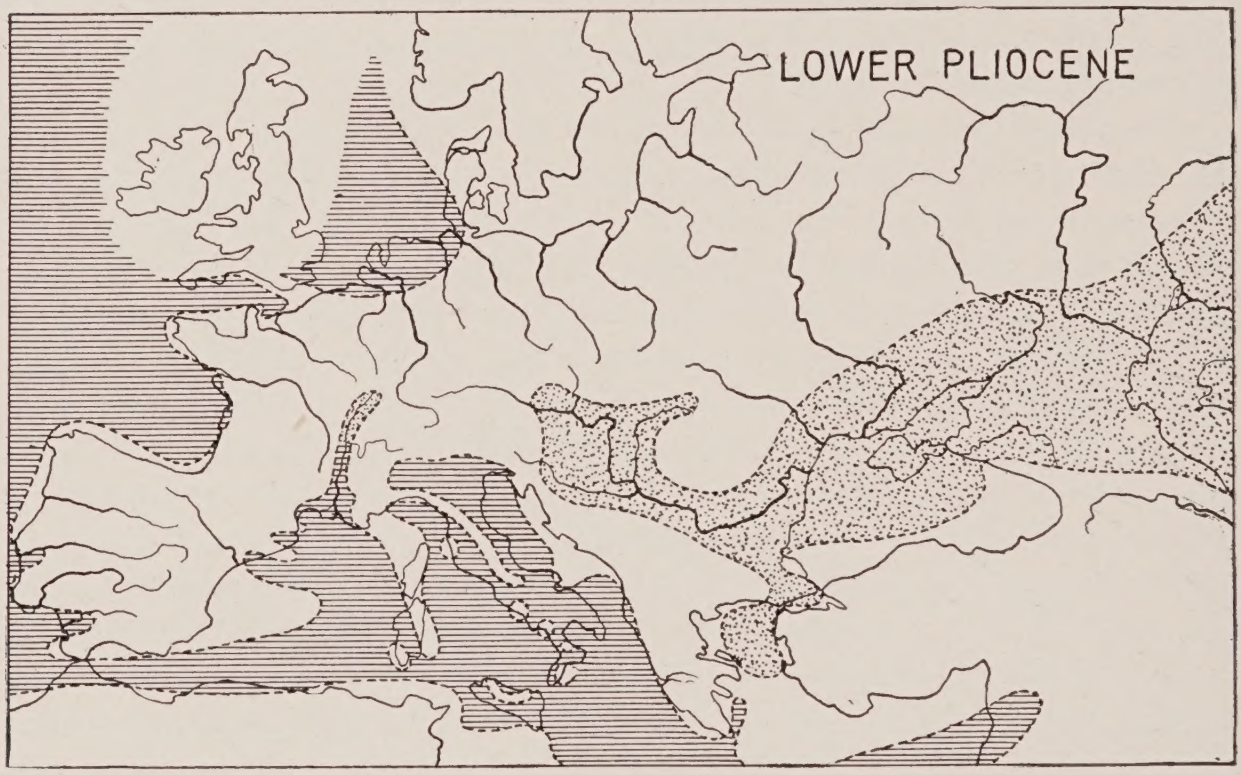


Fig. 152. — Europe in Lower Pliocene or Plaisancian times. White = land. Ruled = sea. Dotted areas = lagoons. After de Lapparent, 1906.

not, however, represent the very base of the Pliocene. At this time southeastern England was connected with France and Belgium by an isthmus, which accounts for the migrations of such continental forms as are recorded in late Pliocene or early Pleistocene stages in Great Britain.[2]

Transition zone. — The lignites of Casino are intercalated in marine (*Congeria*) beds, which form the extreme base of the Pliocene below the '*Marnes Bleues*' of the Plaisancian, so that some Italian geologists regard them as part of the Upper Miocene (Pontian). The mammals of Casino, while mixed, show on the whole a closer affinity to the Lower Pliocene than to the Upper Miocene. Among the surviving Upper Miocene forms is the tapir, *Tapirus priscus*, known also from Eppelsheim. We find *Sus erymanthius*, a boar which occurs likewise at Pikermi; also *Ictitherium*, the hyæna stage of Pikermi. Some of these mammals when more closely studied may, however, reveal a closer kinship to the characteristic Lower Pliocene species such as *Tapirus arvernensis*, *Sus provincialis*, and *Hipparion crassum*. The true Pliocene forms of Casino are the monkey (*Semnopithecus monspessulanus*), an oryx (*Palæoryx cordieri*), a roe deer (*Capreolus australis*), and

[1] Depéret, Succession stratigraphique des Faunes de Mammifères Pliocènes de l'Europe, 1893, p. 539.

[2] De Lapparent, Traité de Géologie, 1906, p. 1637.

a hippopotamus (*H. hipponensis*).[1] It is noteworthy that this species of hippopotamus is recorded (Gaudry, 1876) also in the Pliocene or early Pleistocene of Algeria and in the Siwalik Hills of India.

Outside of Casino, Italy has thus far proved barren of remains of the 'ancient Pliocene fauna,' with the exception of a few scattered fossils belonging to the following characteristic Pliocene species:

(1) *Mastodon arvernensis*, the mastodon of the Val d'Arno.
(2) *Dicerorhinus leptorhinus*, a rhinoceros of Sumatran type, successor to the Upper Miocene types.
(3) *Sus strozzii*, a wild boar.
(4) *Tapirus arvernensis*, a tapir which persists through the Pliocene.

Hippopotami. — The sudden appearance of hippopotami in Europe is one of the most striking features of Lower Pliocene times; it is comparable to that of the sudden appearance of mastodons in Lower Miocene Europe. The presence of these animals in Casino is attested by Depéret (1890) and by Schlosser (1887), the species being described as *H. hipponensis;* an allied form is found in Algeria. These animals are abundant in the Pliocene of the Siwaliks of Asia at this time (p. 329).

The origin of the hippopotami is still unknown. Stehlin[2] (1908) has suggested that possibly the Eocene *Chœromorus* survived beyond the confines of Europe and gave rise to the hippopotami. The affinity of the Siwalik *Merycopotamus*, an animal first described as *Hippopotamus* by Falconer and Cautley, but now placed near the anthracotheres, would appear to suggest an anthracotheroid origin for the hippopotami.

They certainly enjoyed a wide range in Pliocene times from southern Asia to southern Europe and northern Africa. The prevailing Pleistocene species is the giant form known as *H. major*, found in the Upper Pliocene and Pleistocene of Algeria, in southern and central Europe, and in England. The existing African species (*H. amphibius*) is also recorded by some authors in the Pleistocene. The difference is probably only a matter of terms. There are also the dwarf species *H. pentlandi*, *H. minutus*, occurring in the isolated islands of the Mediterranean.[3]

Middle Pliocene or Astian

This stage contains the continuation of the '*faune pliocène ancienne*' of Depéret. Geologically the period is characterized by a gradual recession of the sea and increasing and more widespread fluviatile and freshwater depositions. Fortunately these depositions are rich in mammalian life, so

[1] Depéret, Les Animaux Pliocènes du Roussillon, 1890, p. 189.

[2] Stehlin, H. G., Die Säugetiere des schweizerischen Eocaens. Critischer Catalog der Materialien. Fünfter Teil: *Chœropotamus*, *Cebochœrus*, *Chœromorus*, *Haplobunodon*, *Rhagatherium*, *Mixtotherium*. *Abhandl. schweiz. paläont. Gesell.*, Vol. XXXV, 1908, pp. 691–837.

[3] Von Zittel, K., Handbuch der Paläontologie, 1, IV, Mammalia, Munich, 1891–1893.

that, thanks to the earlier writings of Gervais, Falconer, Forsyth Major, Newton, and Boyd Dawkins, and the more recent researches of Depéret, we get a magnificent picture of the Middle Pliocene life of Europe marking the close of the extension of the older Pliocene fauna. The chief localities are the following:

Roussillon (Fig. 151, 6), a basin surrounding the village of Perpignan, north of the eastern Pyrenees, fluvio-lacustrine deposits.

Meximieux (9), lacustrine tuffs or volcanic ash deposits, famous for flora, in the Saône Valley.

Red Crag of Suffolk (4), fluvio-marine deposits partly of Upper Pliocene age.

The flora of Meximieux, already alluded to on p. 307, shows an abundance of plants with affinities to the genera of the Canary Islands, mingled with those of the Caucasus and of China.[1] Here flourish the bamboo, the sassafras, the magnolia, and the laurel. This indicates a mean annual temperature of 17°–18° C. (62°–64° Fahr.).

The mammalian life of southern France just north of the eastern Pyrenees is preserved in the basin of Roussillon, the site of a Pliocene gulf; in the center of this basin is situated the village of Perpignan. The mammals described below (p. 315) include also those of Montpellier (Hérault), a deposit of marine sands containing a very similar fauna.

We owe to Depéret[2] (1890) a fine analysis of this 'ancient Pliocene fauna.' It is an assemblage which gives us a fair idea of the animal life of the sub-tropical swampy plains of this region toward the middle of the Pliocene period. There are four grand components of the fauna.

(1) The first is that of the surviving Miocene forms (*Machœrodus, Mastodon, Hipparion, Hyœnarctos*) which have left no modern successors.

The other three components are the essentially modern genera or ancestors of genera which still survive and are now distributed in three great zoölogical regions, as follows:

(2) Europe and central Asia, the Palæarctic Region.

(3) The Indo-Malayan province of the Oriental Region.

(4) The Ethiopian or African Region.

The saber-tooth tiger (*Machœrodus*) of the period is of a smaller type than the great Upper Miocene forms. *Hyœnarctos*, the dog-bear (*H. insignis*), is intermediate in structure between the Miocene dinocyons and the true bears, although it is not, as formerly supposed, ancestral to the bears.

The mastodons[3] have now attained a gigantic size and are armed with

[1] De Saporta quoted by De Lapparent, Traité de Géologie, 1906, p. 1645.

[2] Depéret, Animaux Pliocènes du Roussillon, 1890.

[3] Capellini, G., Mastodonti del Museo Geologico di Bologna. *Mem. R. Acad. Sci. Inst. Bologna*, Ser. 6, Vol. IV, Bologna, 1907.

enormously long straight tusks. The especially significant change is that the lower tusks are smaller and that the lower jaws are short or 'brevirostral.' As in North America these mastodons include two series provided respectively with three- and four-crested intermediate molars; of the former 'trilophodont' type is the *M. borsoni*, of the latter 'tetralophodont' type is the *M. arvernensis*. It is noteworthy that these two species persist

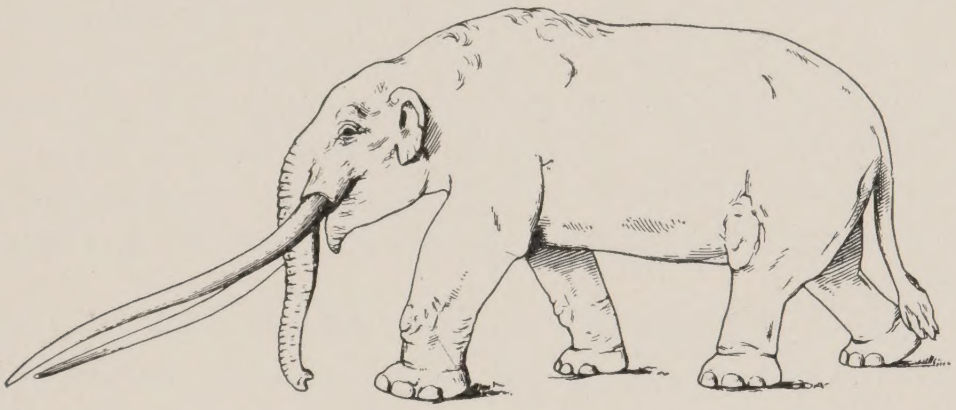


FIG. 153. — Outline restoration of *Mastodon arvernensis*, the great Pliocene short-jawed mastodon of Europe ($\times \frac{1}{72}$).

throughout the Pliocene and that *M. borsoni* is the more closely related to the American Pleistocene mastodon (*M. americanus*), which is also trilophodont.

The tridactyl horse of the period (*Hipparion crassum*) is, like its predecessors, a typical grazing form. There is some recent evidence that this animal persists throughout the Pliocene.[1]

The Oriental and Indo-Malayan element of the fauna of Roussillon and Montpellier includes the two kinds of monkeys, namely, *Dolichopithecus* and *Semnopithecus*, which are related respectively to the macaques[2] and the langurs, both of Asia. We also find that the bear of the period (*Ursus minutus*) is a small member of the *Helarctos* group, ancestral to the arboreal Malayan sun-bear. Similarly the tapir (*T. arvernensis*) is almost identical with the recent Malayan tapir (*T. indicus*) now distributed in Sumatra and Borneo. The two-horned rhinoceros (*Dicerorhinus leptorhinus*) receives its specific name from the slender character of its nasal bones, which are without the supporting septum characteristic of the Upper Pliocene species; it also belongs in the same sub-family (see p. 272) with the existing rhinoceros of Sumatra. The civet (*Viverra*) may be classed with the Indo-Malayan group. Altogether Depéret finds ten species of animals in this fauna which are of existing Indo-Malayan affinity.

The existing African and west Asiatic element is represented by the hyænas (*H. arvernensis*), ancestral to the striped hyæna of north Africa and southern Asia, by the caracals (*Lynx brevirostris*) allied to the southern or

[1] Stehlin, Une Faune à Hipparion à Perrier. *Bull. Soc. Géol. France*, Ser. 4, Vol. IV, 1904, p. 443.

[2] The Barbary ape (*Macacus inuus*) of Northern Africa and Gibraltar is an isolated survivor of these widespread Pliocene macaques.

Persian lynx, by the servals (*Felis christoli*) allied to the recent African forms, by the gazelles (*G. deperdita*) of north African type, slightly smaller than the Dorcas gazelle. The oryx (*Palæoryx cordieri*) is one of the antelopes of a type now abundantly represented in Africa, perhaps ancestral to the existing oryx. The wild cat (*Felis catus aff. maniculata*) is regarded by Depéret as similar to or identical with the caffre cat of northern Africa. Two of the rodent types (*Trilophomys, Ruscinomys*) are allied to the existing crested rats and to the gundis of northern Africa.

The presence of gallinaceous birds (*Gallus*) of a form (*Palæocryptonyx*) allied to the wood quail of Malaysia, of giant land tortoises (*Testudo*), of great river turtles (*Trionyx*), and finally of fish belonging to the Africo-Asiatic group of silurids further accentuates the southern or Ethiopian and Oriental element.

In addition to this essentially southern element there is in the ancient Pliocene fauna a large temperate and north temperate element which allies it with the recent animal life of Europe and of central Asia. The representatives of this element[1] are, among mammals, the fox (*Vulpes*), the wild cat (*F. catus*), the mole (*Talpa*), the shrew (*Crocidura*), the flying squirrel (*Sciuropterus*), the beaver (*Castor*), and the rat (*Mus*). There are hamsters (*Cricetus*), picas (*Lagomys*), boars (*Sus*), roe deer (*Capreolus*), hares (*Lepus*), porcupines (*Hystrix*), otters (*Lutra*); among birds, the goose (*Anser*), the crow (*Corvus*), and the thrush (*Turdus*). It is noteworthy that the fox, mentioned above, is with the exception of the canids, recorded in the Middle Miocene of Œningen, the first true member of the canids to be recorded in Europe, but the wolf also soon appears. At Montpellier (5) in southern France (Hérault) we find, in addition to many of the animals listed above, certain mammals (*e.g. Hyœnarctos, Semnopithecus, Felis christoli, Lutra affinis*) especially recorded. The monkey which occurs here (*Semnopithecus monspessulanus*) is, as above noted, scarcely distinguishable from the langurs of southern Asia. These animals have a shorter muzzle than the macaques, which are represented in the Lower Pliocene by the genus *Dolichopithecus* of Roussillon.

The deer of the period are small forms resembling the existing roe deer, or *Capreolus*, an animal usually provided with only three tines on its antlers; the species *C. australis* persists throughout the Pliocene. Thus the Montpellier mammals in general include a number of survivors (*e.g., Semnopithecus, Palæoryx*) of Lower Pliocene forms of Casino, and a somewhat larger number of species which persist into the Upper Pliocene of the Val d'Arno.

Underlying the typical Upper Pliocene fauna of Perrier has recently been described the 'hipparion fauna' of Roccaneyra.[2] Here occur especially an hipparion of very large size, with slender limbs, a gazelle (*G. julieni*) iden-

[1] Some of these animals are found at Montpellier, but are not recorded at Roussillon.

[2] Stehlin, Une Faune à Hipparion à Perrier. *Bull. Soc. Géol. France*, Ser. 4, Vol. IV, 1904.

tical in dentition with Speke's gazelle of East Africa, also a very large antelope (*A.* aff. *torticornis*), large saber-tooth tigers, hyænas, and wolves (*Canis megamastoides*), the first wolf recorded in Europe. This fauna of Roccaneyra is an open steppe or prairie fauna since it lacks all the characteristic forest-living forms. The geological evidence points to this deposit as of possible Upper Pliocene age, but with this exception there is no support for the idea that hipparions persisted into the Upper Pliocene in Europe.

The date of the introduction of the hippopotamus into Europe, as well as its source, whether Asiatic or African, are very interesting questions. It is recorded at Casino associated with remains of hipparion.

Middle Pliocene
Partial List

Monkeys
  Langurs
  Macaques
Mastodons
Hipparions
Tapirs
Sumatran rhinoceroses
Boars (*Sus*)
Hippopotami
Roe deer (*Capreolus*)
Antelopes (*Palæoryx*)
  of large size
Gazelles (*Gazella*)
Hyænas
Canids (foxes, wolves)
Hyænarctids
  (dog-bears)
Machærodonts
Pandas (*Ailurus*)
Bears
Wild cats, lynxes
Caracals, servals
Flying squirrels
  (*Sciuropterus*)

In the Red Crag (4) of Suffolk, the prevailing animals belong to the ancient Pliocene fauna; this sand deposit of mixed origin contains also some vertebrates (*Equus, Elephas*) probably belonging to higher levels (see p. 321). These remains are chiefly interesting as demonstrating the range westward into Great Britain of this older Pliocene fauna of hipparions, tapirs, mastodons, hippopotami, and roe deer.

The marine mammals of this period found at Montpellier include the sirenians (*Halitherium*), the seals (*Pristiphoca*), three cetaceans (*Delphinus, Rorqualis, Hoplocetus*).

Surveying this older Pliocene fauna as a whole we are struck by the great predominance of animals closely related to existing forms. If the living zoölogist should imagine himself in France at this period, he would see only four animals which would appear entirely novel and unknown, namely, the saber-tooth tiger, the mastodon, the hipparion, and the hyænarctos; all the rest of the fauna would seem to be a very strange commingling, or congress, of African, European, and Asiatic mammals of the present day. Not a single North American element would be observed in this assemblage, unless we except those elements of more remote migration, such as the hares, the tapirs, and possibly the hipparions and the foxes.

Upper Pliocene or Sicilian

With this stage enters the 'newer Pliocene fauna' of English authors, the *faune Pliocène récente* of French authors, a fauna[1] including for the

[1] Depéret, Animaux Pliocènes du Roussillon, 1890, pp. 190–191.

first time the majestic southern elephants (*E. meridionalis*) which herded with the last of the European mastodons and roamed all over Europe from Italy to Great Britain. The tridactyl hipparion disappears, being replaced by the true monodactyl horse (*Equus stenonis*). The larger Etruscan rhinoceros (*Dicerorhinus etruscus*) succeeds the *D. leptorhinus* of the Lower Pliocene. The macaques (*Macacus florentinus*) reappear, closely related to the living apes of Gibraltar. The hippopotami are now widely spread over southern Europe.

Equally striking is the first *appearance* in Europe of the true bovines, ancestors of the existing wild and domestic cattle. The deer also multiply and increase in size, and are especially distinguished by their large and splendidly developed branching horns. Mingled with these new forms are some of the practically unchanged survivors of the ancient Pliocene fauna, such as the saber-tooth tiger (*Machœrodus cultridens*), the bears (*Ursus arvernensis*), the tapirs (*T. arvernensis*), the short-jawed mastodons (*M. arvernensis, M. borsoni*).

This period is, however, sharply defined by the *disappearance* of several members of the earlier fauna, namely, of the Asiatic langur (*Semnopithecus*), the civet (*Viverra*), the panda (*Ailurus*), and the flying squirrels (*Sciuropterus*).

Physiography. — Great Britain is still broadly connected with the continent,[1] so that in the fluvio-marine deposits of the Norwich Crag of Norfolk (p. 321) we find many of the mammals characteristic of northern Italy and central France. The remains of mammals are chiefly preserved in river and lake deposits. There is evidence that the climate is gradually becoming cooler. Among the typical marine formations of Sicily, which give the name to this stage, there is a sudden appearance of shells of northern type, an invasion due to the opening of the Straits of Gibraltar and inflow of Atlantic waters. In the Norwich Crag of England there are also a great many shells of boreal type which increase in number during the latter part of the Sicilian stage. With the cooling of the sea and introduction of northern currents naturally came a lowering of temperature and a retreat of palms and other tropical plants to the south. The dwarf fan palm (*Chamærops*) occurs for the last time on the Lipari Islands, north of Sicily.[1] The advent of the northern types of shells in the sea is prophetic of the Glacial Period.

In the accompanying map (p. 310) is displayed the wide distribution of formations in which the remains of this splendid fauna are preserved (Nos. 10–29). We owe to Forsyth Major (1884, 1890) and to Depéret (1885, 1890, 1893)[2] especially the study of the mammals of the Val d'Arno near Florence, of Olivola in northern Tuscany, and of Perrier (Puy-de Dôme).

The mammals of *Perrier* have been found in gravels at the base of the

[1] De Lapparent, A., Traité de Géologie, 1906, pp. 1648–1652.

[2] For principal titles see Bibliography.

volcanic Mont de Perrier (12), near Issoire.[1] The genera now extinct are here reduced to two, namely, *Mastodon* and *Machœrodus*. All the other mammals of central France of this period, with the exception of the tapirs and antelopes, continued to live on in the same region during the Pleistocene. Monkeys are no longer found in France, a significant evidence of lowering of temperature, but the macaques still occur in northern Italy. While the essentially southern and plains-living antelopes have diminished in number and size, being represented by only two species, the lesser, *Antilope ardea*, the greater, *A. tragelaphus torticornis*, and there is but a single species of gazelle (*G. borbonica*), the essentially northern and forest-living deer have not only multiplied, but have greatly increased in variety and the complication of their antlers. The smaller roe deer (*Capreolus australis*), with its erect three-branched antlers, descended from the *C. matheronis* of the Miocene, persists. There also appears the axis type of deer (*Axis pardinensis*), with three- to four-branched antlers, now characteristic of southeastern Asia. Among the new arrivals is the stag, or red deer type (*C. elaphus perrieri*), with long branched antlers, less complicated, however, than in the Pleistocene and recent true *Cervus*. The fourth deer is of a type (*Polycladus*) now extinct, with elaborately branched antlers, typified by the *C. dicranius* (Nesti). Thus the *Capreolus*, *Elaphus*, *Axis*, and *Polycladus* types are all represented, but the fallow deer, or *Dama* type, which plays a large part in the Pleistocene, has not yet appeared in Europe. The abundance of these browsing forest- and glade-living animals bespeaks a wide extension of the forests at this period. The contemporary *Leptobos etruscus* (= *L. elatus*) is the earliest ox of Europe, a generalized type with long, rounded horn cores, widely separated at their base and placed low down on the forehead; the females originally described as *Leptobos* were hornless; the limbs were unusually slender.

Upper Pliocene
Partial List

Monkeys
  Macaques
Mastodons
Elephants (*Elephas*)
Horses (*Equus*)
Tapirs
Sumatran rhinoceroses
Hippopotami
Cattle (*Leptobos*)
Antelopes and gazelles
  (diminutive)

It is not surprising to find among the enemies of these northern and southern types of ruminants an abundance of both the northern and southern types of Carnivora. Pursuing the deer, appears one of the earliest of the distinctly wolf-like or thoöid canids (*C. megamastoides*). The felids become more varied, including types resembling the lynx, the panther, and the lion. Among these modern carnivores there still survives the saber-tooth tiger (*Machœrodus cultridens*), a species persisting throughout Pliocene times. The bear of Auvergne (*Ursus arvernensis*) is a small animal. The hyænas now include types allied to both the spotted and the striped hyænas

[1] Depéret, C., Considérations générales sur les Vertébrés Pliocènes de l'Europe. *Ann. Sci. Géol.*, Vol. XVII, Paris, 1885, pp. 252–253.

Upper Pliocene
Partial List

Roe deer
Axis deer
Red deer (*Cervus*)
Polycladine deer
Machærodonts

of Africa. The fluviatile otters (*Lutra*) and beavers (*Castor*) are closely allied to existing forms. The small fauna includes voles, picas, hares, porcupines, also species approaching recent types. Among the perissodactyls, the tapirs (*T. arvernensis*) appear in Europe for the last time; the Pliocene tapirs resemble the existing Indian tapirs (*T. indicus*) very closely.[1] The 'Etruscan rhinoceros' is a long-limbed, long-headed animal, distinguished from its Lower Pliocene ancestor (*D. leptorhinus*) by a well-developed bony septum which furnishes support for the great nasal horn; it is structurally related to the *D. platyrhinus* of the Siwaliks of India, as well as to the smaller and much more primitive living species *D. sumatrensis* of Sumatra. This animal survives in the Lower Pleistocene Forest Bed, together with several other members of this fauna. The Asiatic and African element is now less conspicuous than in the older Pliocene fauna.

In his comments on the mammalian fauna of the Val d'Arno, Forsyth Major[2] speaks of the spreading of this fauna eastward into India. Of the types now resident in southeastern Asia the tapir, the axis deer, and the rhinoceros may be mentioned.

The rich fauna of the Val d'Arno is even more varied and typical than that of Perrier. It is splendidly represented in the Museum of Florence. The macaque which occurs here (*M. florentinus*) is the last of the European macaques. The disappearance of the monkeys from Europe at the close of the Pliocene is a very significant fact; it may be remembered that in the Upper Miocene they ranged as far north as Eppelsheim; in the Lower Pliocene they were restricted to the forests of the south of France; in the Upper Pliocene to those of Italy; their gradual southern retreat is probably due to a slowly progressive lowering of temperature.[3]

The elephant of this period, the typical *E. meridionalis* of Nesti, popularly known as the 'southern elephant,' is a magnificent animal with moderately long-crowned or hypsodont molar teeth composed of as many as fourteen rows of closely compressed transverse enamel plates. It is either of Asiatic or African origin. The molars are broad, the enamel thick and smooth. The tusks are of gigantic proportions.

A remarkable feature of the contemporary mastodon (*M. arvernensis*) is the extraordinarily long and very slightly outcurved tusks.[4] The wild

[1] Kittl, E., Fossile Tapirreste von Biedermannsdorf. *Annal. k.k. naturhist. Hofmus.*, Vienna, 1896, Notizen, pp. 57–58.

[2] Forsyth Major, C. J., On the Mammalian Fauna of the Val d'Arno. *Quart. Jour. Geol. Soc. London*, Vol. XLI, June 25, 1884, p. 3.

[3] Boyd Dawkins, W., The Classification of the Tertiary by Means of the Mammalia. *Quart. Jour. Geol. Soc.*, Vol. XXXVI, London, 1880, p. 394.

[4] Capellini, Mastodonti del Museo Geologico di Bologna, 1907.

boar of the period (*S. strozzii*) exhibits tusks more like those of the Asiatic boar (*S. celebensis*) than those of the European boar.

The horse (*Equus stenonis*) which frequented northern Italy in Upper Pliocene times reached a height of nearly 15 hands (1.524 m.); it is distinguished by the narrow anterior pillar (protocone) of the upper molar teeth and is regarded by Ewart[1] as one of the possible ancestors of existing horses, on his theory that these breeds may be traced back to several wild ancestral stocks. Contemporaneous with *E. stenonis* in the Upper Pliocene of Europe was the *E. sivalensis* of the Upper Pliocene of southern Asia, which may also have had a share in the making of modern domestic breeds.

MAMMALS FROM THE RED AND NORWICH CRAGS.[2]

Lutra dubia
Lutra reedii
Phoca moorei
Phocanella minor
Trogontherium minus
Mesoplodon floris
Mesoplodon scaphoides
Ailurus anglicus Dawkins

The *L. dubia* is distinct from the common otter (*L. vulgaris*). The *L. reedii* is of a very brachyodont type, resembling the *L. sivalensis* of India. The seal *Phocanella* agrees with that found in the Belgium Pliocene by Van Beneden. The beaver *Trogontherium minus* is represented by teeth much smaller than those of its successor in the Pleistocene, *T. cuvieri;* its incisor has the front rounded, with rugose enamel, thus differing from *Castor.* The supposed panda, *Ailurus anglicus* Dawkins, from the Red Crag of Suffolk is represented by a perfect upper molar tooth, which strikingly resembles the corresponding teeth of *Ailurus fulgens* of Asia, but is one-third larger in size.

II. PLIOCENE LIFE OF ASIA

Our first glimpse into the life of the forested regions of southern Asia during Miocene times (p. 273) is followed in the Pliocene by a fuller knowledge of what is altogether the grandest assemblage of mammals the world has ever seen, distributed through southern and eastern Asia, and probably, if our vision could be extended, ranging westward toward Persia and Arabia into northern Africa.

It is the most truly cosmopolitan aggregation because in its Upper Pliocene stage it represents a congress of mammals from four great continents, namely: (1) native, or autochthonous mammals of southern Asia, (2) survivals of the fauna known at earlier periods in Europe, presumably common to northern Europe and Asia, (3) mammals of African origin, (4) mammals of North American origin.

By the close of the Pliocene the contributions of these four continents

[1] Ewart, J. Cossar. The Possible Ancestors of the Horse Living under Domestication. *Science*, n.s., Vol. XXX, no. 763, Aug. 13, 1909, pp. 219–223.

[2] Newton, E. T., On Some New Mammals from the Red and Norwich Crags. *Quart. Jour. Geol. Soc.*, Vol. XLVI, Aug., 1890, pp. 444–453.

are thoroughly intermingled. The only continents which do not contribute in the least to this assemblage are South America and Australia.

Hypothetical Original Sources of the Pliocene Life of Southern Asia

1. Natives of Southern Asia	2. Natives of Eurasia	3. Natives of North America	4. Natives of Africa
Anthropoid apes	Bears	Rhinoceroses	Mastodons
Catarrhine monkeys	Porcupines	Horses	Dinotheres
Cavicornia	Mustelines	Tapirs	?Elephants
Cattle (Bovidæ)	Felids	Camels	
Antelopes (Antilopinæ) of Asiatic and African types	Dinocyons	Canids	
	Elotheres	?Wolves and foxes	
Goats (Caprinæ)	Anthracotheres		
Tragulids, or true chevrotains	Chalicotheres		
	True deer		
Cervuline deer			
Axis deer			
Musk deer			
Viverrids or civets			
Hyænas			
Cheetahs (*Cynælurus*)			
Pangolins? (*Manis*)			

Nor does the above list by any means include all the mammals of the south Asiatic Pliocene, because all the small fauna still awaits discovery, the following mammals being conspicuous by their absence in the Pliocene although some of them appear in the Pleistocene.

Mammals Absent or Undiscovered
Insectivores
Lemurs
Marsupials
Hares
Aardvarks
Northern types of deer

Nor, again, are we in a position to list the original homes of the above animals with any degree of finality, the above lists being put forward as tentative.

There are two great areas in which this Asiatic life is known, namely: (1) southern Asia, south of the Himalayas, (2) eastern Asia, China, and Japan.

Eastern Asia, as we shall see, adds considerably to this assemblage, because it includes northerly forms. The continental elevation of the eastern Asiatic coast rendered Japan practically a part of the continent, so that its Pliocene and Lower Pleistocene deposits yield a rich *Stegodon* and *Elephas* fauna. Even Java [1]

[1] Martin, K., Ueberreste vorweltlicher Proboscidier von Java und Banka. *Sammlungen des geologischen Reichs-Museums in Leyden*, Vol. IV, no. 1, 1884, pp. 1–24.

in two localities yields *Stegodon* teeth very similar to *S. ganesa* and *S. insignis;* we find here also *Elephas, Hippopotamus, Sus,* and *Bos.* Even more important is the *Pithecanthropus erectus* discovered by Dubois in 1894, with its decided affinities to the line of human ancestry.

1. Life of Southern Asia

This life is revealed in the wonderfully rich deposits broadly known as the 'Siwaliks,' vast ancient flood plain areas stretching for a distance of fifteen hundred miles along the foothills of the Himalayas. To assist

Fig. 154. — Chief Miocene and Pliocene fossil mammal deposits of Asia. **1**. Maragha, Persia. **2**. Perim Island. **3**. Manchhar Beds of Sind. **4**. Siwaliks of the Punjab. **5**. Sub-himalayan Siwaliks (River Brahmaputra to River Jhelum). **6**. Valley of the Lower Irawadi, Burma. **7**. Miocene and Pliocene deposits of China (Provinces of Shan-si, Shen-si, Sze-chuan, Kwang-Tung, Ho-nan, Hu-nan, Hu-peh). **8**. Miocene and Pliocene deposits of Japan.

our mental picture of the environment it is important to remember that while the elevation of the Himalayas commenced with the Tertiary epoch, the range only attained an elevation comparable to that which it now possesses toward the commencement of the Pliocene period (Oldham and Blanford).

Our knowledge of the Siwalik mammals is due chiefly to the masterly researches of Falconer and the recent revisions of Lydekker. The geologic or time succession of the various deposits which have been treated collectively as of this age is of the utmost importance but still awaits careful

analysis. So far as can be judged from the most valuable geologic notes and discussions of Oldham,[1] Blanford,[2] Lydekker,[3] and recently of Schlosser,[4] the general arrangement of these beds in ascending geologic order is somewhat as follows:

		Fauna II
Irawadi Valley, Burmah (Pliocene)		Stegodons Horses (*Equus*) Camels Buffaloes (*Bubalus*)
Sub-Himalayas	'Upper Siwaliks' (Upper Pliocene)	
	'Lower Siwaliks' (Middle and Lower Pliocene, Upper Miocene)	
	Punjab 'Siwaliks' (Middle and Lower Pliocene, Upper Miocene)	Fauna I Anthracotheres Mastodons
	Island of Perim, west coast of India (Miocene and Pliocene)	
	Bugti Hills of Baluchistan (Middle and Upper Miocene)	
	Manchhar Beds of Sind (Middle and Upper Miocene)	

Geologic or Stratigraphic Succession of the Mammals

The mammals of the 'Lower Manchhar' beds of Sind have already (p. 273) been shown to be of Middle and Upper Miocene age; those of the Bugti Hills of Baluchistan appear to partake of the same character, namely, what may be called the *Anthracothere Zone* fauna. The mammals of the Island of Perim, on the west coast of India, appear to be transitional, that is, to contain both this older Anthracothere and a newer *Hipparion Zone* fauna. As we ascend through the Punjab Siwaliks, through the 'Lower Siwaliks' and the 'Upper Siwaliks' of the sub-Himalayas, into the Siwaliks of the Irawadi Valley, Burmah, the anthracothere fauna gradually disappears, and is gradually replaced by the newer, or true Pliocene fauna. Only in the 'Upper Siwaliks' of the sub-Himalayas and in the Irawadi Valley, Burmah, do we find the pure Upper Pliocene fauna of *Stegodon*, *Elephas*, *Equus*, *Camelus*, and *Bubalus*. These beds are partly successive; they partly overlap in time.

Perim Island, a small reef overlaid by ossiferous conglomerates (fluviatile), contains fragmentary remains of mammals discovered by von Hügel in 1836. It lacks the Upper Pliocene forms entirely and appears to be intermediate between the Lower Manchhar Zone of Sind, and to correspond only with the lower, true Siwaliks; it contains none of the Upper Siwalik mammals.

[1] Oldham, R. D., A Manual of the Geology of India. Calcutta, 1893.

[2] Blanford, W. T., Homotaxis as Illustrated from Indian Formations. *Rec. Geol. Surv. India*, Vol. XVIII, Pt. 1, 1885.

[3] Lydekker, R., A Geographical History of Mammals. Cambridge, 1896.

[4] Schlosser, M., Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. *Abh. k. bayer. Akad. Wiss.*, Cl. II, Vol. XXII, Pt. 1, Munich, 1903.

In northwest India fossils occur low down in the Punjab Siwaliks which attain a total thickness of 14,000 feet. It is by no means certain, observes Oldham, that some of the specimens from the northwestern Punjab, especially those with mid-Tertiary affinities, are not confined to the lower levels. The precise horizon of all the forms collected is not known; a very large proportion of Siwalik remains were obtained by native collectors,

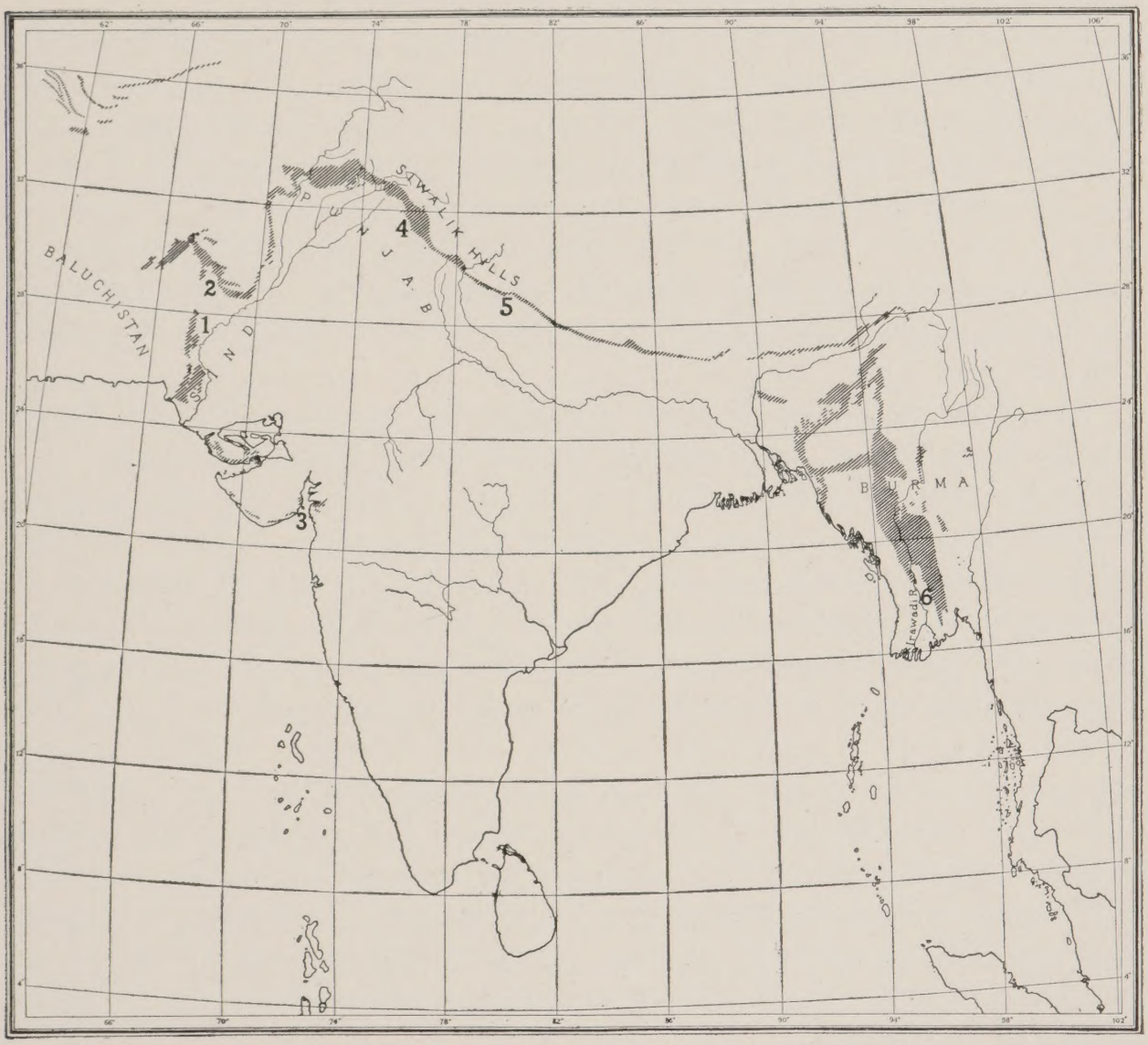


FIG. 155. — Map of India showing Tertiary formations containing fossil mammals (oblique lines). **1**. Manchhar Beds; **2**. Bugti Hills; **3**. Perim Island; **4**. Punjab Siwaliks; **5**. Sub-himalayan Siwaliks; **6**. Beds of the Lower Irawadi. After Oldham.

and the localities are of course doubtful. While these Punjab beds are distinguished from the Miocene fauna of the Lower Manchhar by the rarity of anthracotheres and the absence of *Hyotherium*, they appear to contain a somewhat older fauna than the true Siwaliks of the sub-Himalayas. Thus, of the surviving Miocene forms several are recorded in the Punjab only, namely: *Dinotherium*, *Machœrodus*, *Dorcatherium*, anthracotheres. More primitive mastodons are also chiefly from the Punjab.

The Siwalik Group, or Siwaliks proper, are exposed in the sub-Himalayas, a long range of hills which for a distance of 1,500 miles advance along

the main chain to the south. The group reaches the enormous aggregate thickness of 15,000 feet. The clays, sandstones, and conglomerates of which it is composed were probably deposited by the flood plains of great rivers which flowed from the Himalayan chain by the same outlets as their modern representatives;[1] thus there is a close resemblance between these beds and the recent deposits of the flood plain of the Ganges.[2]

Here again in the 'Lower Siwaliks' are recorded certain surviving Miocene forms such as the giant dogs (*Amphicyon*), the clawed perissodactyls (*Ancylotherium*), supposed entelodonts (*Tetraconodon*), and the bear dogs (*Hyænarctos*). In the 'Upper Siwaliks,' or higher Siwalik strata only (Oldham), occurs the Upper Pliocene fauna including the true horse (*Equus*), the first camels (*C. sivalensis*), the stegodont elephants (*S. insignis, S. ganesa*), and the giant tortoises (*Colossochelys*). Especially modern in these highest strata is the buffalo (*Bubalus palæindicus*), closely similar to the buffalo of the Ganges and central provinces of India at the present time.

The Irawadi Valley of Burma apparently contains only the Upper Siwalik fauna and an intermingling even of Lower Pleistocene types.

It thus appears probable that the 'survival theory' of the intermingling of Oligocene, Miocene, Lower and Upper Pliocene types in India contains some elements of truth, but has been overstated because of erroneous or incomplete field records. As well observed by Oldham, some of the anomalies would probably disappear if we knew the horizons. At the same time, the balance of evidence is all in favor of regarding the Siwaliks proper as of Upper Miocene and Lower, Middle, and Upper Pliocene age. While it is not certain that there were Oligocene survivals in the Pliocene of Asia, it is certain that animals which became extinct at the close of the Miocene in Europe, such as the amphicyons, chalicotheres, dinotheres, the aceratheres, the teleocerine rhinoceroses, the entelodonts or elotheres, survived in Asia. Otherwise the general law of genetic succession or replacement of more ancient by more modern types prevailed in Asia as in Europe.

It is premature to attempt to work out the genetic or stratigraphic succession of these mammals, which will furnish one of the most fascinating problems for the British palæontologist. The fauna is of such deep import in connection with the life of Europe, Africa, and North America, that it is desirable to examine it in some detail.

General Characters of the South Asiatic Mammals

A broad survey proves that, as indicated on p. 322, southern Asia was a center of the evolution of the anthropoid apes of the Old World and

[1] Geikie, A., Text-Book of Geology, p. 1021, London, 1893.

[2] Oldham, R. D., A Manual of the Geology of India. Calcutta, 1893.

catarrhine monkeys, of the grand divisions of the hollow-horned ruminants or Cavicornia, and, if not the chief center, it was at least an extremely important center of the evolution of the Proboscidea, because here we find these animals in all stages of transition between the mastodon and the elephant type. It remains to be discovered whether a similar fauna and similar evolution characterized Africa at this time.

Among the primates we find the orang (*Simia*), an ape now confined to Borneo and Sumatra, also the chimpanzee (*Anthropopithecus*), another ape now confined to Africa, the Siwalik species displaying a more human type of dentition than that of the existing African form. Among the monkeys are the macaques (*Macacus*) and langurs (*Semnopithecus*), which we have also seen in the 'ancient Pliocene' fauna of Montpellier. There are also true baboons (*Cynocephalus*).

The assemblage of Carnivora is the most extraordinary the world has ever seen. There are first the ancient bear-like canids *Amphicyon* and *Hyænarctos*, related to Miocene types of Europe. The felids include machærodonts (*Machærodus, Ælurogale, Æluropsis*), beside varieties of true cats (*Felis*) analogous to the leopard and lynx, and including species equaling the tigers in size. There are five species of hyænas, including primitive forms resembling the Upper Miocene *Ictitherium* of Pikermi, while others of more modern aspect are similar to the spotted hyæna (*H. crocuta*), and still others to the striped hyæna (*H. striata*). Among the smaller carnivores are civets (*Viverra*), otters (*Lutra*), ratels (*Melivora*), bears related to the Indian sloth bear (*Melursus*), foxes (*Vulpes*), and wolves (*Canis*).

Among the few rodents known are representatives of the bamboo rats (*Rhizomys*), porcupines (*Hystrix*), and the hares (*Caprolagus*).

The variety of odd-toed ungulates is no less remarkable. Among these perissodactyls are first to be noted the aberrant chalicotheres (*?Ancylotherium*), which also survive in the Pliocene and possibly into the early Pleistocene of China. The tapirs (*Tapirus*) are rare, being recorded only in the Upper Siwaliks of the Irawadi Valley. Of the rhinoceroses, the aceratheres include a widely distributed species (*A. blanfordi*), also found in the Upper Miocene of Maragha in Persia, as well as a possible (Lydekker) teleocerine rhinoceros (*T. perimense*). Related to the dicerorhine or Sumatran phylum of rhinoceroses, which we have observed from the early Miocene onward in Europe, is the majestic *D. platyrhinus;* while we find also representatives of the true Asiatic rhinoceroses (*R. palæindicus*), related to the existing one-horned types of India and Java and not represented in Europe at all.

Two species of *Hipparion* are known, and it appears certain that this animal, which does not certainly extend beyond the Middle Pliocene of Europe, survived into Upper Pliocene times in Asia; in Africa it is said to have survived into the Lower Pleistocene. One species (*H. antilopinum*)

is said to have lost its lateral digits. Here also in the Upper Pliocene of the sub-Himalayan Siwaliks occurs a species of true horse. This ancient Siwalik horse (*E. sivalensis*) measured about 15 hands (1.524 m.); it had long, very slender limbs, a long, tapering face, deflected to form an angle of nearly twenty degrees with the base of the cranium; it seems also to have had a long neck, high withers, and a high-set tail, thus resembling the so-called Arabian, or desert type of horse. Like the *E. stenonis* of the Pliocene of northern Italy it may have contributed to modern breeds,[1] such as the unimproved Kirghiz races of central Asia. It is distinguished from *E. stenonis*, however, by a broad protocone, or anterior pillar, on its upper molars (see p. 321).

Among the artiodactyls in the period of the 'Upper Siwaliks' the most significant new arrival from America is the camel (*C. sivalensis*), said to retain affinities with the South American llamas (*Auchenia*). There are also true giraffes (*Camelopardalis*), and a great variety of the extinct horned giraffes known as sivatheres, bramatheres, and vishnutheres, allied to but much more specialized than those of the Upper Miocene of Pikermi; it is noteworthy that these aberrant giraffes are the only ruminants which give an archaic character to the artiodactyl fauna of the Siwaliks, all the remaining Artiodactyla being decidedly modern in aspect. Among the actually modern forms are the true chevrotains (*Tragulus*) and musk deer (*Moschus*). There are also more ancient forms said to be allied to the Miocene *Palæomeryx* of Europe. The distribution of water chevrotains (*Dorcatherium*) in this fauna of European affinity is probably confined to the older or lower beds. The higher deer are all of existing Asiatic type, namely, representatives of the rusa (*C. sivalensis*) and axis group. It is noteworthy that there are no deer of the northern (*Cervus*) type.

The Cavicornia, or hollow-horned ruminants, are represented by an enormous variety of forms closely related to those now confined to Asia or to East and South Africa, but also found in North Africa in Pleistocene times. Among the animals related to the existing Asiatic antelopes are the nilgai (*Boselaphus*), the four-horned antelope (*Tetracerus*), the gazelle (*Gazella*). Among animals of modern African affinity are the elands (*Oreas*), the kudus (*Strepsiceros*), the roan and sable antelopes (*Hippotragus*), forms related to the hartebeests (*Bubalis*) and water bucks (*Cobus*), also the gazelles (*Gazella*). It is these African types only which have allies in the European 'newer Miocene' fauna of Pikermi and Maragha, — a significant fact. Especially novel is the appearance of the goats (*Capra*) in forms closely related to existing species of Asia, also including a large hornless goat (*Bucapra*) with bovine affinities.

All these facts point to northern India as a great center of adaptive

[1] Ewart, J. C., The Possible Ancestors of the Horses Living under Domestication. *Science*, n.s., Vol. XXX, no. 763, Aug. 13, 1909, pp. 219–223.

radiation of the Cavicornia. This is rendered still more probable through the appearance here of a great variety of bovines. The ancestor of the Indian buffalo (*Bubalus*) is here found in a flat-horned species (*B. platyceros*) recorded both in the Punjab and in the southern Himalayas; the remaining bovines are of remarkably modern type and appear first in the sub-Himalayas only. They include a short-headed bison (*Bison sivalensis*), the earliest known member of this phylum, the small cattle (*Hemibos*) related to the existing anoa of the Celebes, also some long-skulled forms such as the ancestral ox (*Leptobos*), said to be similar to the species (*L. etruscus*) which first makes its appearance in the Val d'Arno in the 'recent Pliocene fauna' of Europe. Here too are found three species of true oxen (*Bos*), the earliest known ancestors of the domestic cattle. As regards migration, it is important to note that the bison (*Bison*) and the true oxen (*Bos*) appear in Europe only after the opening of Pleistocene times (Forest Bed), namely, during the second faunal stage.

The pig family, which we have seen represented in the Miocene Manchhar beds of Sind by *Hyotherium*, here branches out into a great variety of forms including many species of true pigs (*Sus*), of the 'horse-pig,' or *Hippohyus*, with extremely elongate or hypsodont molars, and of the peculiar sanithere (*Sanitherium*). Among the surviving forms in the Punjab Siwaliks are, as identified, both the listriodonts (*Listriodon*), long-snouted pigs confined to the Miocene of Europe, and an aberrant branch of the entelodonts or elotheres (*Tetraconodon*), giant pigs confined to the Oligocene of Europe and North America. Both of these identifications if correct are of the greatest interest. An ancient character is also given to the entire Siwalik series by the specialized anthracothere *Merycopotamus*, long-snouted, flat-skulled animals which are confined to the Siwaliks or true Pliocene, whereas the anthracotheres proper, *Anthracotherium* and *Hyopotamus*, are only recorded in the Manchhar beds and Bugti Hills of Sind. *Merycopotamus* is considered a representative of an early branch of the anthracotheres, from which the hippopotami may have taken origin.

Among the river-living forms is the primitive hippopotamus with six teeth in the front part of the jaw (*Hexaprotodon*), said to be allied to animals which are found in the Pliocene and Pleistocene of Algeria (*H. hipponensis*); there is also the true hippopotamus (*H. iravadicus*), found in the 'Upper Siwaliks' of the Irawadi Valley of Burma.

The Proboscidea include first the dinotheres found in the lower levels (*Dinotherium pentapotamiæ, D. indicum*), descendants of animals known in the Manchhar beds of Sind and on the Island of Perim, surviving into the older Punjab Siwaliks, and closely related to *D. giganteum* of the Upper Miocene of Europe. Second, there are the mastodons, third the stegodons, and fourth the true elephants.

Evolution of the Proboscidea

The true Proboscidea exhibit a great range of evolution, from the conservative phylum of *trilophodont* mastodons (related to the *Mastodon americanus* of the American Pleistocene) through intermediate stages in which the number of transverse crests on the grinders steadily increases, until we reach the *Stegodon* stage, in which there are from six to twelve low transverse crests on the grinding teeth; finally into elephants which embrace both (1) the African, or *Loxodonta* type (*E. planifrons*) with narrow grinding teeth having comparatively short crowns and few transverse crests, and (2) the Indian elephant, or *Elephas* type (*E. hysudricus*), which is said to be closely related to the southern mammoth (*E. meridionalis*) of the Upper Pliocene and Pleistocene of Europe.

The evolution of these remarkable mammals is evidently *polyphyletic* and involves a great number of contemporaneous changes in the skull, tusks, and grinders, among which the following are the most important: (1) abbreviation or increasing brachycephaly of the skull; (2) abbreviation of the lower jaws and loss of the lower tusks; (3) loss of the enamel of the upper and lower tusks; (4) addition of transverse crests on the intermediate and posterior grinding teeth in both jaws; (5) transition from a short-crowned, brachyodont browsing adaptation of the grinding teeth of the true mastodon type into the long-crowned hypsodont grazing adaptation of the elephant type; (6) addition of a 'cement' coating to the grinders.

Arranged in *ascending order* of complexity,[1] as observed in the older, intermediate, and newer Miocene and Pliocene formations of Asia, these animals may be listed as follows:

Euelephas hysudricus, a primitive hypsodont elephant of the Indian type, related to *E. meridionalis* of Europe.

E. (*Loxodonta*) *planifrons*, a hypsodont elephant of the African type, related to *E. antiquus* of the Pleistocene of Europe.

Stegodon insignis (=*S. ganesa*), sub-hypsodont, with as many as thirteen transverse crests, found also in China, Japan, and Java, Upper Pliocene and Lower Pleistocene.

Stegodon bombifrons, brachyodont, with as many as nine transverse crests, found also in China.

Stegodon cliftii, brachyodont, closest to *Mastodon*, found also in China and Japan.

Mastodon (*Tetralophodon*) *sivalensis*, molars with four to five transverse crests and cement.

Mastodon (*Tetralophodon*) *perimensis*, molars with four transverse crests and some cement.

Mastodon (*Tetralophodon*) *punjabiensis*, molars with four transverse crests.

[1] In each case the word 'molars' refers to the 'intermediate molars.'

Mastodon (Tetralophodon) latidens, molars with four transverse crests.
Mastodon (Trilophodon) falconeri, molars with three transverse crests.
Mastodon (Trilophodon) pandionis, molars with three transverse crests.
Mastodon (Trilophodon) palæindicus, molars with three transverse crests, a variety of *Trilophodon angustidens.*
Mastodon (Trilophodon) angustidens.

A diphyletic subdivision of the mastodons is: (1) into those forms in which the transverse crests are composed of conic nipples, or tubercles, with accessory cones, forming trefoils, namely : *M. (Tetralophodon) longirostris, M. pentelici, M. (Tetralophodon) sivalensis;* and (2) those in which we find simple, sharply defined transverse crests without accessory cones, *M. (Trilophodon) turicensis, M. (Trilophodon) borsoni.*

The trilophodont species belong in the same group with the *M. (Trilophodon) borsoni* and the *M. (Trilophodon) turicensis,* characteristic of the Upper Miocene of Europe, while the tetralophodont mastodons are related to the *M. (Tetralophodon) longirostris* of Europe. It will be recalled (p. 254) that the trilophodont *T. angustidens* has large lower incisors, while the trilophodont *T. turicensis* has small lower incisors. In all the tetralophodonts of Europe and Asia, including India and China, the upper incisors are without enamel, while the lower incisors are small or wanting, and the lower jaw is correspondingly abbreviated; this abbreviation of the lower jaw is a characteristic feature of the Pliocene mastodons.

A progressive character not mentioned above is the addition of cement to the grinding teeth, as in horses and other grazers; this we first discover in certain of the tetralophodonts (*T. perimensis*), and it increases in the stegodonts (*S. cliftii, S. bombifrons*).

It is a remarkable feature of the proboscideans that from the geologically lowest to the highest or most recent forms they all use their six grinding or premolar-molar teeth on each side *at some period of life;* while the lower forms employ four and even five grinders at once, it is a distinctive, progressive character of the highest forms to employ their upper and lower grinders successively, two pairs at a time, and finally one pair at a time, the anterior grinders being used in youth and the posterior in old age.

The stage *E. (Loxodonta) planifrons* is the final transition between the mastodontoid, or crested, and the elephantoid, or plated type; the grinders consist of high, thin transverse crests with intermediate valleys completely filled with cement. This animal is much more primitive than the *E. antiquus,* or straight-tusked elephant of the Lower Pleistocene of Europe, the closest counterpart of *E. antiquus* being found in the *E. namadicus,* which is recorded in the Lower Pleistocene of India.

It is obvious from this review that part of the mastodons of India resemble the Middle and Upper Miocene mastodons of Europe, and it would appear that the Upper Pliocene of India (? and of Africa) witnessed

the first occurrence of the true elephant (*E. hysudricus*), just as the Upper Pliocene of Europe witnessed the first occurrence of the southern mammoth, or true elephant (*E. meridionalis*).

Conclusions as to the age of the Siwalik Fauna. — Against the actual Upper Miocene age of any of the true Siwalik fauna is the fact, to which attention was called by Forsyth Major,[1] that there is not a single species in common with the Upper Miocene of Pikermi. Yet it would appear that the true Siwalik fauna begins with mastodons, hipparions, chalicotheres, rhinoceroses, dinotheres, antelopes, amphicyons, closely comparable to Upper Miocene forms of Europe. The Upper Siwaliks close with true elephants (*Elephas*), camels, buffaloes, and cattle, also true horses (*Equus*), which are of Upper and Lower Pliocene but not of Lower Pleistocene age. The successive evolution stages of these mammals will undoubtedly be discovered when the horizontal or geographic and vertical or stratigraphic distribution is carefully worked out. This is one of the most fascinating problems awaiting British palæontologists.

It is important to note, as an indication of the tropical conditions of climate of northern India in Pliocene times, the presence of a large number of mammals which have now been driven farther south into the Indian archipelago and into Africa, especially the anthropoid apes and certain of the antelopes. It is equally important to note the absence of northern forms of deer and other ruminants. The single species of bear known in the Upper Siwaliks of the Irawadi is of southern type, similar to the existing Indian sloth bear (*Melursus*). Traces of this northern forest fauna are to be found in China.

Outlyers of this south Asiatic fauna are to be found on the north in China, and on the west, in beds of Maragha, Persia, and even in Africa.

As noted by Schlosser [2] we find at Maragha, near the southern shore of the Caspian Sea, pure Asiatic types, such as the sivathere (*Urmiatherium*), the hornless giraffe (*Alcicephalus*), the true giraffe (*Camelopardalis*), three species of antelope, the Asiatic hipparion (*H. richthofeni*) and the acerathere (*A. blanfordi*). On the other hand, out of thirty-two Maragha species, thirteen of the most typical occur at Pikermi. Thus the fauna of Maragha may be said to form a transition between the Asiatic and Chinese assemblages and those of Pikermi and Samos. While it shows distinct affinities with Asia, it contains at the same time some northern (*i.e.* north Asiatic) elements.

2. Life of Eastern Asia

The earliest mention of fossils in China dates back to 1853, when Davidson published a short notice on a number of teeth sent to England from

[1] Forsyth Major, *Comptes rendus, Acad. Sci. Paris*, Nov. 16, 1891.

[2] Schlosser, M., Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. *Abh. k. bayer. Akad. Wiss.*, Cl. II, Vol. XXII, Pt. 1, Munich, 1903.

Shanghai. Thus the extinct life of China and of western North America was brought to the notice of scientists at about the same time, but the literature on the former still consists of a small number of mostly incomplete studies. Owen published a small work in 1870; Gaudry in 1871; there is a monograph by Koken (1885); Lydekker has contributed various notes, and finally Schlosser[1] in his *Die fossilen Säugethiere Chinas* (Munich, 1903) has made a more exhaustive study of all the material available to him, comparing the Chinese faunas with the contemporary animal life of Europe and southern Asia (Schlosser, *op. cit.*, pp. 7, 8). In this illuminating review of the fossil mammals thus far recorded in China[1] we obtain our first picture of the life of northeastern Asia in Upper Miocene and Pliocene times. It is important to note that there are practically no geologic records.[2]

It is a world of life which has close relationships with that of Persia (Maragha) and diminishing resemblances as we pass westward to the faunas of Samos, of Pikermi, Greece, and of Mont Léberon, France. It naturally has its closest relationships with the life of southern Asia, as seen in the Siwalik fauna. The Siwalik fauna, as we have seen, however, belongs to more southern latitudes and contains anthropoid apes which have been referred both to the chimpanzees and orangs, beside other mammals distinctive of southerly latitudes and represented at the present time by descendants which inhabit southern Asia and Africa. Not only is the more northerly life of China of somewhat hardier type, but its closer proximity to North America is evidenced by the presence of forest horses (*Hypohippus*), of supposed camels (*Paracamelus*), and of supposed teleoceline rhinoceroses (*Teleoceras*).[3] Conspicuous by their absence are certain characteristic Miocene, European, and Siwalik forms, such as *Amphicyon*. It is noteworthy that no cattle are found in this fauna, no animals related to the genera *Bos*, *Bison*, or *Bubalus*.

The age of these scattered deposits is late Miocene or early Pliocene. They are broadly characterized by abundant remains of the north Asiatic hipparion (*H. richthofeni*), of hornless rhinoceroses, or aceratheres, of very large browsing horses, or anchitheres, which possibly are identical with

[1] Schlosser, M., Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. *Abh. k. bayer. Akad. Wiss.*, Cl. II, Vol. XXII, Pt. 1, Munich, 1903.

[2] In all the larger cities of China, fossil remains are sold as 'dragon bones' and 'dragon teeth,' and used in medicine. To bring out their supposed medicinal properties they are fried, boiled in wine, or even eaten in their natural state as a cure for diseases of the heart, kidneys, liver, and intestines, and are further regarded as very beneficial in nervous affections. Nearly all collections of Chinese fossils have been bought up from the druggists, who fortunately keep accurate records as to the provinces and even localities from which the materials have been brought (Schlosser, 1903, pp. 3–6).

[3] Some of the other animals from China, figured by Schlosser, singularly resemble allied American types, *e.g. Hipparion richthofeni*, *Equus sivalensis* (= *Pliohippus*), *Sus microdon* (= *Prosthennops*). The rhinoceroses generally are very similar to American forms. (Note by W. D. Matthew.)

the *Hypohippus* of the Miocene of America, of trilophodont and tetralophodont mastodons, besides a varied group of ruminants, including giraffes, gazelles, antelopes, and kudus similar to those known in the Upper Miocene of Maragha, Persia. There are also certain types which characterize the older Pliocene fauna of Europe, such as the fox (*Vulpes*) and the hyæna.

These mammals are divided by Schlosser into: (1) an open plains or *steppe fauna*, found in the red clays of the provinces of Shan-Si (northern China) and Sze-Chuan (western China), perhaps also in Kwang-Tung and other eastern provinces; and (2) a *forest fauna*, chiefly preserved in the red sandstones and greenish limestones of the provinces of Ho-Nan and Hu-Peh (central China), and probably also in the neighborhood of Tientsin (northeast).

Schlosser believes that the remains of the open plains fauna were probably washed into pools without being transported far from the places where the animals died. The larger number of hipparion remains have been found with the open plains mammals, although this widely distributed tridactyl horse also occurs associated with the forest animals; a dwarf race and also a larger one are known. Of the rhinoceroses, the species *R. habereri* is regarded as possibly related to the short-legged *Teleoceras* type of America and western Europe. The aceratheres belong to a species (*Aceratherium blanfordi*) found both in the Manchhar beds of Sind, in the Siwaliks of India, and in Maragha, Persia. In the forest fauna are recorded two other kinds of rhinoceroses, one of which is referred to the two-horned Sumatran, or *Dicerorhinus* type, and the other (*R. brancoi*) to the one-horned Indian or true rhinoceros type which is recorded also in the Manchhar beds of Sind (p. 275) and in the Siwaliks.

Of the giraffes the gigantic *Camelopardalis* (=*Giraffa*) is similar to that from the Pliocene Siwaliks, while the hornless giraffe, *Alcicephalus*, and the sivathere, *Urmiatherium*, are identified with the Upper Miocene giraffes of Maragha. The gazelles are both steppe-living types, with resemblances to the small Middle Pliocene gazelle (*G. deperdita*) of Roussillon, France, and to the existing Grant's gazelle of Africa. Two distinctively Upper Miocene antelopes of Pikermi type, namely, *Palæoreas* (eland) and *Tragocerus* (flat-horned antelope) are also recognized here. Antelopes resembling the addax (*Plesiaddax*) and kudu (*Strepsiceros*) are also reported, as well as antelopes suggesting the nilgai (*Boselaphus*) of modern India. In association with these plains types have been found a number of remains of Pliocene hyænas, including three closely allied species, one of gigantic size, also an extinct hyæna (*Palhyæna*) intermediate in structure between the Pikermi form (*Ictitherium*) and the true hyænas.

The Proboscidea are exclusively mastodons, being referred to the trilophodont (*M. pandionis*) and tetralophodont (*M. latidens*) types similar to those which are found in the Manchhar beds of Sind as well as in the Punjab or Lower Siwaliks.

Especially interesting in the forest fauna are ancestral true deer of medium and small size, and belonging to several species. To the forest fauna too is referred the fox (*Vulpes*) which, we shall find (p. 308), is first recorded in the older Pliocene of Europe, the otter (*Lutra*), badger (*Meles*), and the characteristic Miocene and Pliocene saber-tooth tigers (*Machærodus*), similar to forms discovered at Pikermi and Eppelsheim, are also found here. To the forest fauna Schlosser likewise attributes the mastodon, two kinds of two-horned rhinoceroses (*Dicerorhinus*), a forest-living gazelle (*Gazella*), and several species of *Sus*.

It is noteworthy that a true horse of south Asiatic type (*Equus sivalensis*), as well as the gigantic camel *Paracamelus*, are also included in this older fauna. We have seen that *Equus*[1] is a distinctive feature of the Upper Pliocene both of Europe and Asia. It would appear possible that the association of these animals of more advanced evolution with the older Pliocene or Upper Miocene types may be due to an error in the geologic records.

Other very characteristic forms inhabiting China, of which the geologic age reference in the present writer's opinion is somewhat doubtful, are the chalicotheres (*Ancylotherium sinense*), the tapirs (*T. sinensis*), and the hippopotami. Schlosser considers both the tapir (*op. cit.*, p. 73) and the chalicothere (*op. cit.*, p. 75) as Pleistocene. The survival of the latter animal into Pleistocene times is a record of exceptional interest; it rests upon somewhat slender evidence.

3. Pleistocene of India

The Karnul Caves in the district of Madras, southeast India, as studied by Lydekker,[2] give us a picture of south Asiatic life in Pleistocene times. The fauna as a whole has lost the greater part of its cosmopolitan Pliocene aspect, and closely resembles the typical Oriental fauna of modern India; however, it still retains a certain affinity with the African fauna, particularly in the presence of a baboon (*Cynocephalus*), of the spotted hyæna (*Hyæna crocuta*), of a small equine very similar to the Abyssinian ass (*Equus asinus*), and a pangolin indistinguishable from the recent giant pangolin (*Manis gigantea*) of west Africa. Most of the Asiatic species represented in these caves are now extinct, but they have a less primitive aspect than the forms of the Upper Pliocene of the Narbada Valley. The Asiatic elements include monkeys, tigers and leopards, jungle cats, viverrines, sloth bears, porcupines, and mice. Among the larger Herbivora, beside the wild ass of African type there is an ass similar to the existing south Asiatic onager (*E. onager*). The rhinoceros presents affinities to the

[1] Many of the specimens referred to *Equus* probably belong to the older evolutionary stage.

[2] Lydekker, R., The Fauna of the Karnul Caves. Indian Tertiary and Post-tertiary Vertebrata. *Pal. Ind., Mem. Geol. Surv. India*, Ser. 10, Vol. IV, Pt. 2, 1886.

Upper Pliocene Etruscan type of Europe. The ruminants include buffaloes, nilgais, gazelles, black bucks, antelopes resembling the oryx, four-horned antelopes, sambar and axis deer, muntjacs, chevrotains, the wild boar, and wild pigs. With the upper layers of animal remains traces of man are found, and even at the lower levels are found primitive implements.

III. PLIOCENE LIFE OF NORTH AMERICA

The close of the Miocene and opening of the Pliocene cannot be dated in the western plains region of North America as in Europe, because while in Europe there is a marked interruption in the conditions of life at the close of the Miocene, in the western plains and mountain regions of North

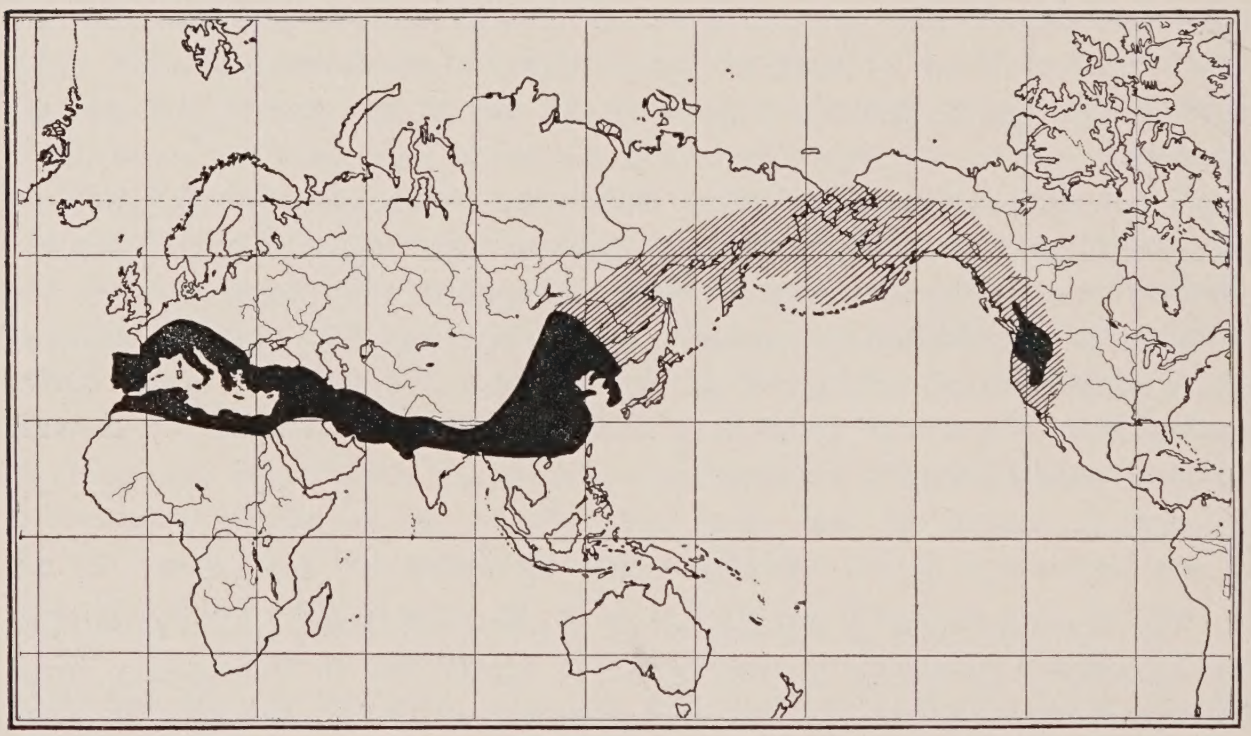


Fig. 156. — Upper Miocene and Pliocene distribution of the Strepsicerine and Hippotragine Antelopes. Known distribution in black, hypothetical migration area in oblique lines.

America both the conditions of life and the mammalian fauna continue without a break. This, like the American passage from the Oligocene to the Miocene and that from the Miocene to the Pliocene, is an artificial one, made for purposes of convenience and of correlation with the Old World time scale.

As regards the time scale, a new feature of paramount importance and interest arises in connection with the sudden and welcome extension of our knowledge of the mammals of North America to the far southeast, along the ancient seacoast of Florida. Here appear for the first time in North America means of correlation such as characterize European formations throughout, namely, the alternation of marine shell-bearing formations with freshwater mammal-bearing formations. The former contain invertebrates which may be closely compared with those of

Europe; the latter contain mammals which may be closely compared with those of the Western plains. This coincidence is observed in the opening of the Pliocene in the formation known as the 'Alachua Clays,' and again in the close of the Pliocene in the 'Peace Creek' beds, both of which mammal-bearing formations have been described in relation to their surrounding shell-bearing formations by the expert invertebrate palæontologist, Dr. W. H. Dall. The fauna and relations of these formations will be described below.

Relations with Eurasia. — The mammals of the American Pliocene are the least known of all the American epochs. Early in the Pliocene the typical Cavicornia, or hollow-horned ruminants of Eurasia, first make their appearance in North America in forms somewhat similar in appearance to the *Protragocerus* of the Miocene of Europe. In the Upper Pliocene we have seen that the camels of North America first make their appearance in India and China. With these exceptions we know of no very grand or marked interchanges of life between the New and Old Worlds in this period until the very close, when the Old World elephants appear.

American migration of Asiatic antelopes. — The appearance of true Asiatic antelopes related to two of the great sections, the tragelaphine and hippotragine, is one of the most recently discovered and profoundly impressive features of Pliocene times. The first certain evidence of this kind is the supposed hippotragine antelope *Neotragocerus* discovered by Matthew and Cook in western Nebraska in 1908 [1]: this animal is believed to be related to the same group as the *Tragocerus* of the Upper Miocene of Pikermi, a group now represented by some of the largest and finest African antelopes in the region south of the Sahara, including the roan antelope (*Hippotragus equinus*), the sable antelope (*H. niger*), the oryx, and the addax. The horn is short and straight, with a round-oval cross section.

By permission of the New York Zoölogical Society.

FIG. 157. — A recent hippotragine type of Africa, the sable antelope (*Hippotragus niger*).

This evidence of American invasion by true Asiatic antelopes was brilliantly and amply confirmed during the summer of 1909 by Merriam's

[1] Matthew, W. D., and Cook, H. J., A Pliocene Fauna from Western Nebraska. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVI, no. 27, 1909.

discovery[1] in the Virgin Valley, Nevada, of antelopes (*Ilingoceros*) with spirally twisted horn cores, related to the kudus (*Strepsiceros*) of the tragelaphine section, the section represented to-day by the nilgai of India, as well as bush bucks and harnessed antelopes, the sitatungas, kudus, and elands of Africa. There are a number of species of these twisted-horn types as well as an oval-horned genus (*Sphenophalos*). The type specimen of *Ilingoceros* resembles the *Protragelaphus* of the Pliocene of Europe and Asia. Thus we have definite proof of the existence in the Western plains and mountain region in Pliocene times of considerable if not of great herds of antelopes of Asiatic and African type. The bearing of this discovery on the zoögeographic relations of the New and Old Worlds in the Pliocene is very significant.

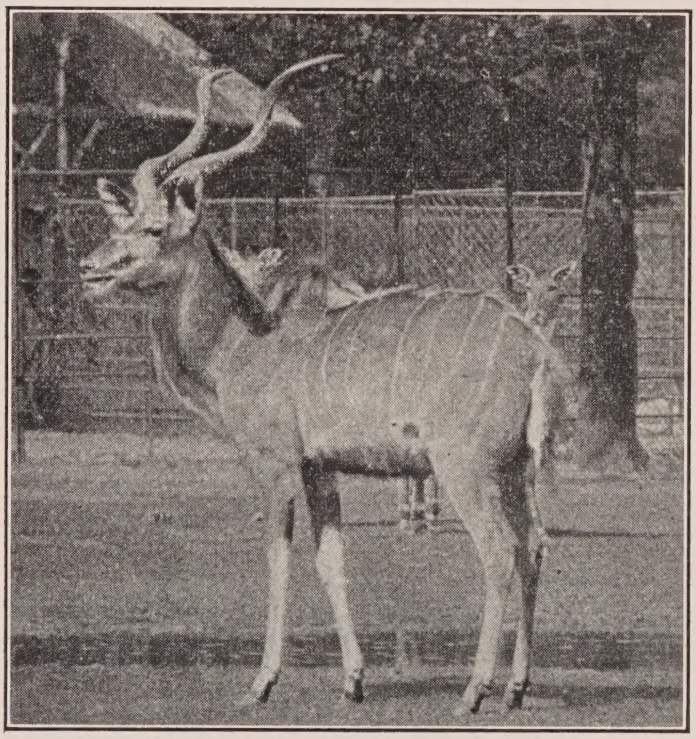


Fig. 158. — A recent strepsicerine antelope of Africa, the kudu (*Strepsiceros kudu*). After Gambier Bolton.

Extinction and chronology. — The attempt to form New and Old World parallels brings up the question of the value of extinction in determining geologic time. Was there a world-wide extinction of the teleocerine rhinoceroses at the close of the Miocene, or did these animals survive into Pliocene times in America as well as in Asia? The answer is that there is considerable but not as yet conclusive evidence that the teleocerine rhinoceroses reached their highest development and extension in the Lower Pliocene of America and Asia. The same remark applies to the giant dogs, or amphicyons, which disappear in the Upper Miocene of Europe, but are found in the supposed Middle Pliocene or Blanco beds of Texas, and are also recorded in the Pliocene of Asia. The clawed perissodactyls, the chalicotheres, disappear in the Upper Miocene of Europe and North America, but survive in Asia even into the Pleistocene, according to Schlosser.[2] A great number of mammals of various kinds survive in southern Asia after they disappear in Europe and North America. The conclusion is that extinction *per se* is of little value in geologic synchronism.

[1] Merriam, J. C., The Occurrence of Strepsicerine Antelopes in the Tertiary of Northwestern Nevada. *Univ. Cal. Publ., Bull. Dept. Geol.*, Vol. V, no. 22, Dec., 1909, pp. 319–330.

[2] Schlosser, M., Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. *Abh. k. bayer. Akad. Wiss.*, Cl. II, Vol. XXII, Pt. 1, Munich, 1903.

Reunion with South America. — As the Pliocene was an epoch of elevation of all the continents, it affected eastern North America after some oscillations, but before the termination of the marine Pliocene the permanent connection of the peninsula of Florida with the North American continent was accomplished.[1]

After an interval of separation which, so far as the mammal record goes, extended back to the Upper Cretaceous or Basal Eocene, South America became again united with North America, and an interchange of mammals took place; some physical, climatic, or biotic barriers were undoubtedly removed. The previous separation need not have been at Panama, as is generally assumed [2]; Hill [3] believes that from the close of the Oligocene onward the waters of the Atlantic and Pacific have been separated at this point; in other words, that the Isthmus of Panama is as old as the Oligocene. Ortmann [4] has suggested the adoption of von Ihering's hypothesis [5] that the water barrier existed for a long period across the parallel of the present Amazon River.

The supposed discovery of the remains of large sloth-like or gravigrade edentates in the Middle Miocene (Mascall) of Oregon and in the Lower Pliocene (Alachua Clays) of Florida makes it appear possible that these mammals were resident in North America throughout the Age of Mammals, but this does not remove the significance of the great invasion of these animals from South America in Lower and Middle Pliocene times. In this connection Scharff's hypothesis [6] should be considered. (Compare p. 93.)

Evidence of fish faunas. — As regards the theory of a long prevailing separation of North and South America in Cænozoic times, the freshwater fishes, on the whole, supplement the evidence afforded by the mammals. Eigenmann [7] (1906) makes the statement that North America has not contributed a single element to the freshwater fish fauna of South America. This, however, should be compared with the statement on p. 136. The beginnings of intercommunication are shown by the fact that two prominent South American families, the Characinidæ and Cichlidæ, have at the present time representatives as far north as the Rio Grande River, while

[1] Dall, W. H., Geological Results of the Study of the Tertiary Fauna of Florida. *Trans. Wagner Inst.*, Vol. III, Pt. 6, 1903, p. 1550.

[2] Matthew, W. D., Hypothetical Outlines of the Continents in Tertiary Times. *Bull. Amer. Mus. Nat. Hist*, Vol. XXII, Art. xxi, 1906, p. 365.

[3] Hill, R. T., Geological History of the Isthmus of Panama and Portions of Costa Rica. *Bull. Mus. Comp. Zoöl.*, Vol. XXVIII, 1908, p. 270.

[4] Ortmann, A. E., Von Ihering's Archiplata-Archelemis Theory. *Science*, n.s., Vol. XII, no. 311, Dec. 14, 1900, p. 929.

[5] Von Ihering, H., The History of the Neotropical Region. *Science*, n.s., Vol. XII, no. 310, Dec. 7, 1900, pp. 857–864.

[6] Scharff, R. F., On an Early Tertiary Land-Connection between North and South America. *Amer. Natural.*, Vol. XLIII, Sept., 1909, pp. 513–531.

[7] Eigenmann, C. H., The Fresh-water Fishes of South and Middle America. *Pop. Sci. Month.*, June, 1906, pp. 515–530.

several members of the North American fauna have representatives as far south as the Isthmus of Tehuantepec.

It is true that the existing North American fish fauna is almost entirely distinct from the tropical American fauna; the latter has its affinities with the fishes of tropical Africa, and in Eigenmann's opinion necessitates a former land connection between Africa and South America. Such a mid-Atlantic land connection would be known as 'Atlantis,' and while of a highly hypothetical character, it is interesting to note that fresh evidence in its favor has recently been brought forward by J. W. Gregory.[1] This writer maintains that the striking similarity of the West Indian corals to those of the Miocene deposits of the Mediterranean basin and to the living genera of the Red Sea can only be explained on the assumption that there was a shallow water connection across the Central Atlantic at a period no later than the Miocene. Moreover, this fauna could not have come by way of the North because it is absent from the northern Miocene of Europe and America.

The geographic distribution of land mammals does not favor such an hypothesis, although it is a convenient one for certain facts of distribution, such as the occurrence of the water snake *Pterosphenus* in the Fayûm and in Eocene beds of Alabama, the distribution of the characines, cichlids, siluroids, and probably of the octodont rodents. Likewise an archipelago between western Africa and eastern America might have facilitated the migration from Africa to America of the sirenians and the zeuglodonts in Eocene times; but such migrations may equally well have occurred by way of the Pacific coast line and through the gulf between the continents. A south-Atlantic connection with Africa is quite another matter, which has been discussed above under Antarctica (p. 75).

Geologic Succession

Our knowledge of the mammals of the Pliocene epoch in America is very incomplete and still awaits the more active exploration and exact research which have so nearly solved the mammalian succession of the Miocene and earlier periods. The historic or geologic succession also requires more exhaustive study.

The formations which yield us vistas of Pliocene life in North America are widely scattered, limited in extent, and less rich in complete fossil remains than those of the Miocene. Despite the evidence afforded by the invertebrate palæontology of Florida, there is some doubt as to whether certain of these older formations, here provisionally referred to the Pliocene, do not more properly belong in the Upper Miocene, where they have been previously placed.

Somewhat the same feeling prevails as to the age of the beds assigned

[1] Gregory, J. W., Contributions to the Palæontology and Physical Geology of the West Indies. *Quart. Jour. Geol. Soc.*, Vol. LI, no. 22, 1895, pp. 255–312.

to the close of the Pliocene in the following table; they may prove subsequently to belong rather to the early part of the Pleistocene.

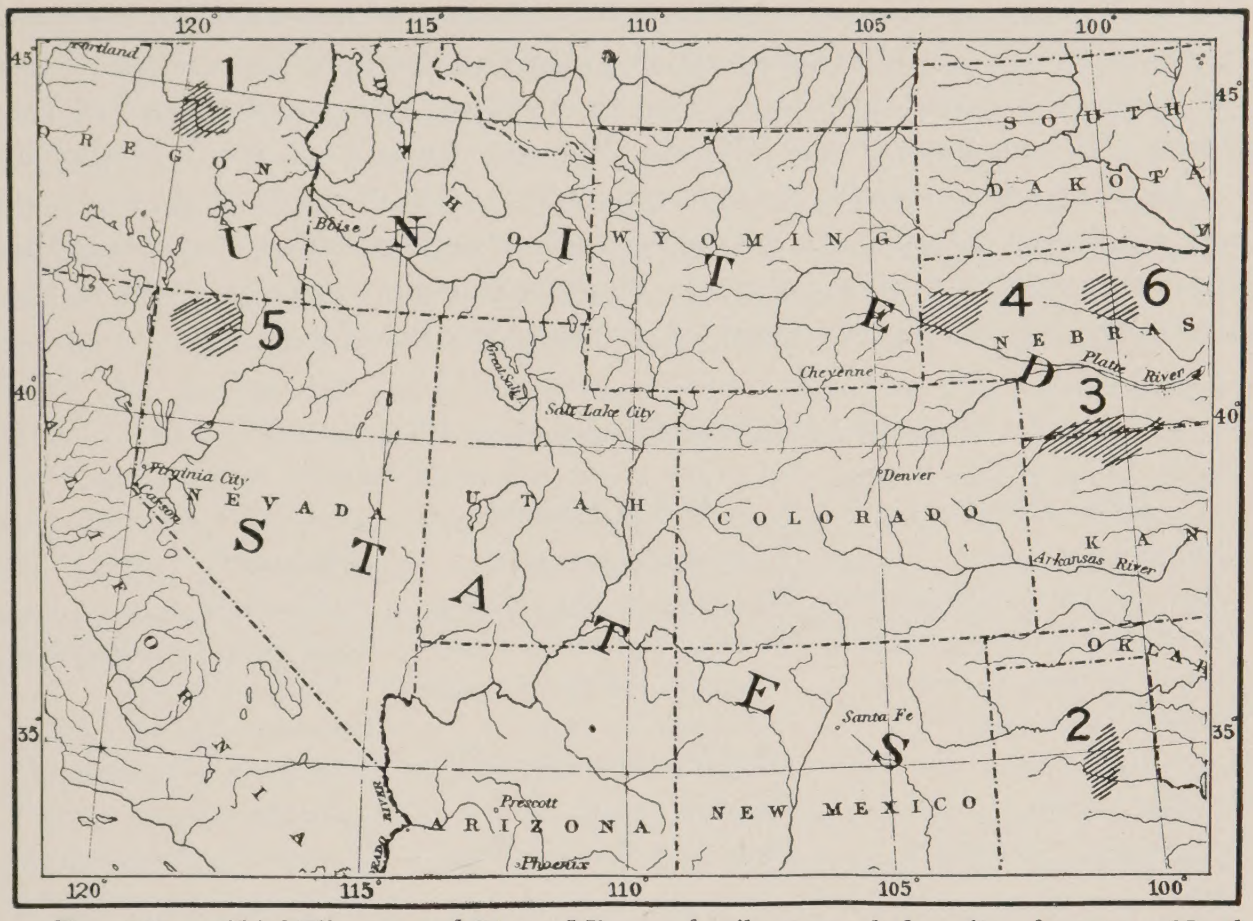


FIG. 159. — Chief Pliocene and Upper Miocene fossil mammal deposits of western North America. **1**. Rattlesnake, Oreg. **2**. Blanco, Tex. **3**. Ogallala, Kan., Nebr. **4**. Snake Creek, Nebr. **5**. Virgin Valley, Nev. **6**. Loup River, Nebr. (See text for horizons.)

With these doubts in mind as stimulating to further research, the following ascending arrangement of the best known formations is set forth provisionally:

Upper Pliocene, or Lower Pleistocene	*Peace Creek* Formation of southern Florida,	*Elephas? columbi* and *Equus* Zone
	Loup River, of eastern Nebraska	*Elephas imperator* and *Equus* Zone
Middle Pliocene	*Blanco* Formation, Staked Plains, or Llano Estacado, of Texas	*Glyptotherium* Zone, *Rhinoceros* extinct or undiscovered
Lower Pliocene	Virgin Valley and Thousand Creek of Nevada	*Ilingoceros* Zone, *Rhinoceros* surviving
	Snake Creek beds, western Nebraska	*Neotragocerus* Zone, *Rhinoceros* surviving
	Rattlesnake Formation, John Day Valley, Oregon	*Alticamelus* Zone, *Rhinoceros* surviving
	Alachua Clays, northern Florida.	*Peraceras* Zone, *Rhinoceros* very abundant
Lower Pliocene, or Upper Miocene	*Republican River* Formation, northern Kansas and Nebraska.	*Peraceras* Zone

It is important to note that Matthew and Merriam have compared the 'Snake Creek' and 'Virgin Valley' faunas with that of Pikermi, or the Upper Miocene of Greece (p. 267). It is obviously premature to attempt to correlate these subdivisions with the Pliocene stages of Europe, yet there seems to be a broad correspondence in America with the divisions of the 'Older Pliocene Fauna' and 'Newer Pliocene Fauna' of the Old World.

As in all other epochs, subdivisions will be finally made with clearness and exactness through the successive extinctions of older forms and the successive arrivals of newer forms. Pending this more exact research of the future, the following provisional subdivision may be offered:

Provisional Subdivision of American Pliocene Life

Lower Pliocene	*Middle Pliocene*	*Upper Pliocene*
Rhinoceroses aceratherine, teleocerine	Rhinoceroses extinct	Elephants (*Elephas*)
'Giraffe' or browsing camels	Browsing horses extinct	Grazing and monodactyl horses (*Equus*)
True or grazing camels	Grazing horses of *Protohippus*, *Pliohippus*, and *Hipparion* type	Browsing camels extinct
Earliest Cavicornia	Gigantic browsing camels	True grazing camels and llamas only
Browsing horses	Grazing camels	Mastodons disappear in the western plains region
Grazing horses	Short-jawed mastodons	Tapirs disappear in the western plains region
Long-jawed mastodons		
Tapirs		

Climatic and Physiographic Conditions

Great Plains. — There is evidence, both in the sandy nature of the deposits in the Great Plains region, in the extinction of browsing types of horses and camels, and in the survival of grazing types in the same families, of increasing aridity in the Western plains and mountain region. This was probably accompanied by more widely prevailing summer droughts and by the contraction of the streams during the dry season. It is certainly significant that the rhinoceroses, brachyodont or browsing horses, and giraffe or browsing camels successively disappear. In the early Pliocene or in the close of the Miocene we find proofs (Sternberg [1]) of the existence of great herds of large land tortoises moving slowly across the plains. Their presence in such large numbers is in itself proof of arid conditions, and it is an interesting bit of collateral testimony from palæobotany that seeds, found within a fossil skull of one of these animals, belong to a species of plant (*Tithymalus willistoni*) which, according to Cockerell,[2] indicates an open, relatively arid, although not strictly desert country.

[1] Sternberg, C., Letter.

[2] Cockerell, T. D. A., Letter to the author, April, 1909.

California. — In the Pliocene of the Pacific coast[1] a change to colder conditions is indicated both by the disappearance of warm-temperate types of plants and by the colder character of the salt water fauna, as well as of that found in the freshwater Pliocene lake beds. The whole west coast of North America was rising and the shore receding westward; the waters of the Pacific no longer reached the foot of the Sierra Nevadas, nor even the great central valley between the Sierra Nevadas and the Coast Range; but elevation was not uniform, for valleys of the coast ranges that had been eroded during the Miocene were filled with sediments during the Pliocene; the enormous deposits to a depth of 3,000 feet of the Great Valley between the Sierras and the Coast Range belong partly to the Pliocene and partly to the Quaternary, an area wholly of fluviatile origin. Thus during the Pliocene the Sierra Nevadas were elevated, and California at that time was very much like the California of to-day; with the great mountain ranges of the Sierras on the east, the long, broad valley — in many cases covered by freshwater lakes — in the center, and on the west the long, low Coast Range.

The Pliocene Flora

The eastward trend of the deciduous tree flora of Europe is a most significant fact. It has been pointed out above that the Miocene and Pliocene forest trees of Europe become the modern forest trees of our Central and South Atlantic states. With the flora in late Tertiary times there came certain faunal waves. Unfortunately nothing is known of the flora of the Great Plains region nor of the central mountain region, and we must rely upon observations made in California, from which only indirect conclusions can be drawn.

Flora of California. — Here we must rely upon the earlier notes of Lesquereux (1859–1888) and of Turner (1891).

Plants of the auriferous gravels of the Sierra Nevada[2] collected in Nevada County, California, on the thirty-ninth parallel indicate a temperature a few degrees higher on the average than that of middle California of the present day; in other words, they represent a latitude a few degrees farther south. Thus in Nevada County on the thirty-ninth parallel in Pliocene times there lived palms similar to those which now flourish in California on the thirty-fourth parallel. Pliocene palms are, however, very rare, only a single specimen of a sabal being found in the whole collection from Nevada County. The prevalence of a warmer climate than the present in Pliocene times seems to be indicated by oaks of Mexican type and by species of figs (*Ficus*), but this is counterbalanced by the presence of the birch (*Betula*),

[1] Smith, J. P., Salient Events in the Geologic History of California. *Science*, n.s., Vol. XXX, no. 767, 1909, pp. 346–351.

[2] Lesquereux, L., Report on the Fossil Plants of the Auriferous Gravel Deposits of the Sierra Nevada. *Mem. Mus. Comp. Zoöl. Cambridge, Mass.*, Vol. II, 1882.

the beech (*Fagus*), the elm (*Ulmus*), which are all characteristic northerly types. We conclude that the Pliocene climate in this region was like that of the Gulf of Mexico, or zone of the live oak, at the present time. It is likely that the region of Chalk Bluffs, Nevada County, in Pliocene times was sheltered by western ranges of mountains against the influence of Pacific fogs; at all events, the absence of conifers seems to indicate a drier climate. A very striking feature of this flora is that which it possesses in common with the Pliocene flora of central Europe, namely, that it contains a large number of trees which no longer grow on the Pacific slope of North America but are now confined to the Atlantic slope. Among these are species of the sweet gum (*Liquidambar*), of the magnolia, of the prickly ash (*Zanthoxylum*), and of the holly (*Ilex*).

Some indication of the general age of this flora is found in the fact that out of forty-two species, twelve are closely allied to Miocene types, while thirty are more closely related to the present flora, especially of the Eastern or Atlantic States. The conifers, including the sequoias, which are now the most conspicuous element of the Sierras, did not exist, or at best were very rare, in Pliocene times in California (Lesquereux, 1882).

The most recent contribution to the Pliocene flora of California is that of Turner,[1] who records the following plants of Kirker Pass, California, latitude 38°, as of Pliocene age: the date plum (*Diospyros*), the magnolia (*Magnolia*), the laurel (*Laurus*), and the viburnum (*Viburnum*). The same author notes that the flora from Corral Hollow, California (latitude 38°), referred by Lesquereux to the Miocene, is, however, probably of Pliocene age, as it is found associated with Pliocene shells. This flora includes horsetails (*Equisetum*), sequoias (*Sequoia*), yews (*Taxites*), alders, chestnuts, willows, poplars, planes, laurels, cinnamons (*Cinnamomum*), myrtles (*Myrtus*), red bays (*Persea*), and sumac (*Rhus*).

Sirenians on the Pacific coast.[2] — Other indications of mild climatic conditions are found in the presence of mammals remotely allied to the manatees and dugongs of the present equatorial belt. The remarkable littoral or marine mammal known as *Desmostylus* derives its name from the clusters of rounded and heavily enameled columns which constitute its grinding teeth. The muzzle is slender and tapering, and armed with one pair of incisors in the upper jaw and two pair in the lower. It is a large animal, the skull being eighteen inches to two feet in length. According to Merriam it is found only in marine formations of Pliocene age. It certainly inhabited both the eastern and western shores of the Pacific coast; remains have been found in California, Oregon, and Japan.

[1] Turner, H. W., 1891. Geology of Mount Diablo. *Bull. Geol. Soc. Amer.*, Vol. II, 1891, pp. 396–397.

[2] Marsh, O. C., Notice of a New Fossil Sirenian, from California. *Amer. Jour. Sci.*, Vol. XXXV, 1888, pp. 94–96.

Flora of the Eastern states. — Lesquereux[1] also described a flora from Graves County, Kentucky (latitude 37°), which he believed to be of Pliocene age, including the fig (*Ficus*), laurel (*Laurus*), soapberry (*Sapindus*), and the oak (*Quercus*). In the Pliocene of Bridgetown, New Jersey, the following plants have been found: the sweet gum (*Liquidambar*), laurel, and poplar. One of the earliest of the numerous contributions of the same author is that on the supposed Pliocene flora collected near Somerville, Tennessee.[2] This flora finds its relatives at the present time on the southern shores of Florida and islands of the Gulf of Mexico; there are only four plants referable to existing species. It includes the laurel, the wild orange tree (*Prunus*) now found in the Bahamas and near the coast of the Carolinas, the oak of a species now found along the coast of Florida, the beech, a species of more northern range, and the willow.

Late Miocene or Early Pliocene

In every branch of life the fauna from northwestern Kansas to Florida is a continuation and evolution of the typical Miocene fauna of North America. Perhaps it is Miocene, for there are no new elements. The clawed perissodactyls or chalicotheres are absent or undiscovered, while the oreodonts (*Merycochœrus*, *Merychyus*) are becoming rare; conditions were either becoming unfavorable for these forms in this region or the entire phylum was dying out. The rarity of the browsing horses is an indication of conditions unfavorable to the older brachyodont browsing types; a few remains of these animals are, however, still found. It is important to grasp clearly the fact that the grazing horses are now in a highly polyphyletic condition.

The chief formations in which these late Miocene or early Pliocene early types of mammals occur are the following:

4. *Rattlesnake Formation* of John Day Valley, Oregon.
3. *Republican River Formation* of northwestern Kansas.
2. *Alachua Clays* or *Archer Formation* of northern Florida.
1. *Ogallala Formation* (typical) Darton, of southwestern Nebraska.

Late Miocene or early Pliocene times in North America were characterized by the survival of the last members of the great family of oreodonts, which are thus far represented only by fragmentary specimens of the characteristic Miocene genera *Merycochœrus* and *Merychyus*. Among the perissodactyls the browsing or forest horses (*Hypohippus*) still survive but are also becoming rare; they are represented by forms with somewhat longer teeth than those of the Middle Miocene. Of the grazing horses the char-

[1] Lesquereux, L., Recent Determinations of Fossil Plants from Kentucky, Louisiana, Oregon, California, Alaska, Greenland, etc., with Descriptions of New Species. Compiled and prepared for publication by F. H. Knowlton. *Proc. U.S. Nat. Mus.*, 1888, pp. 11–38.

[2] Lesquereux, L., On Some Fossil Plants of Recent Formations. *Amer. Jour. Sci. and Arts.*, 2d Ser., Vol. XXVII, May, 1859, pp. 359–366.

acteristic horses of the Miocene *Merychippus* stage, with grinding teeth of intermediate length, still survive in almost equal numbers with the more progressive grazing horses, *Protohippus*, *Pliohippus*, and *Neohipparion*. The rhinoceroses are represented by the teleocerine and aceratherine phyla, both of which reach a high degree of specialization. Of these the aceratheres or hornless rhinoceroses are represented by species of *Aphelops* comparable in evolution to the *Aceratherium blanfordi* of the Pliocene of Asia as well as by the short-headed *Peraceras*. The teleocerine rhinoceroses, which are also believed to survive in the Pliocene of Asia, although extinct in Europe, attain their maximum evolution and size, and are present in great number and variety. The aberrant perissodactyl chalicotheres have apparently disappeared in North America, though it is possible that some of these animals will be unearthed by future exploration, since they are believed to have survived in Asia in Pliocene times.

Indicative of the Upper Miocene rather than of the Lower Pliocene age of this fauna is the fact that the trilophodont and tetralophodont mastodons still retain the long lower jaws or longirostral character of the Miocene mastodons of Europe and America, whereas the Lower Pliocene mastodons of Europe are referred to the short-jawed species *M. arvernensis;* this specific reference, however, may not be correct, so that too much stress should not be laid upon this single feature.

Among the camels *Pliauchenia* is now the characteristic genus; this is a typical grazing camel with affinities to the llamas of South America, as the name indicates. We also find surviving the short-limbed or grazing camel *Procamelus*. The browsing or giraffe camel (*Alticamelus*) still occurs.

In the earliest of these supposed Pliocene formations, namely, the 'Republican River' of Kansas and 'Alachua Clays' of Florida, we have discovered no evidence of the existence of the Cavicornia or hollow-horned ruminants of the Old World type. The older formations, therefore, contain rhinoceroses, but do not contain, apparently, the antelopes or Bovidæ.

The Alachua Clays or 'Archer Beds' of Florida

These clays were so named by Dall in 1885.[1] They had been referred by some authorities to Upper Miocene, by others they had been regarded as late as Pliocene or even Pleistocene. They appear on the western anticline of the higher portions of Alachua County (Fig. 160), along the banks of many rivers and streams, occurring in sinks, gullies, and other depressions, in rocks of successive age. The clays are of a bluish or grayish color, and extremely tenacious. The deposits were believed by Dr. J. C. Neal (1883) to have occurred along the margins of an ancient lake, which he named Lake De Soto. The existence of such a Pliocene lake or series of

[1] Dall, W. H., and Harris, G. D., The Neocene of North America. *Bull. U.S. Geol. Surv.*, no. 84, 1892.

lakes is indicated by such scanty evidence as is here afforded. Whether such a lake existed or not is less important than the conclusion reached by Dall in his report of 1892[1] that the beds underlying the Alachua Clays at certain points are not of Miocene but of early Pliocene age. The same author (*op. cit.*, p. 130) concludes, "While the determination of the precise epoch of the deposition of

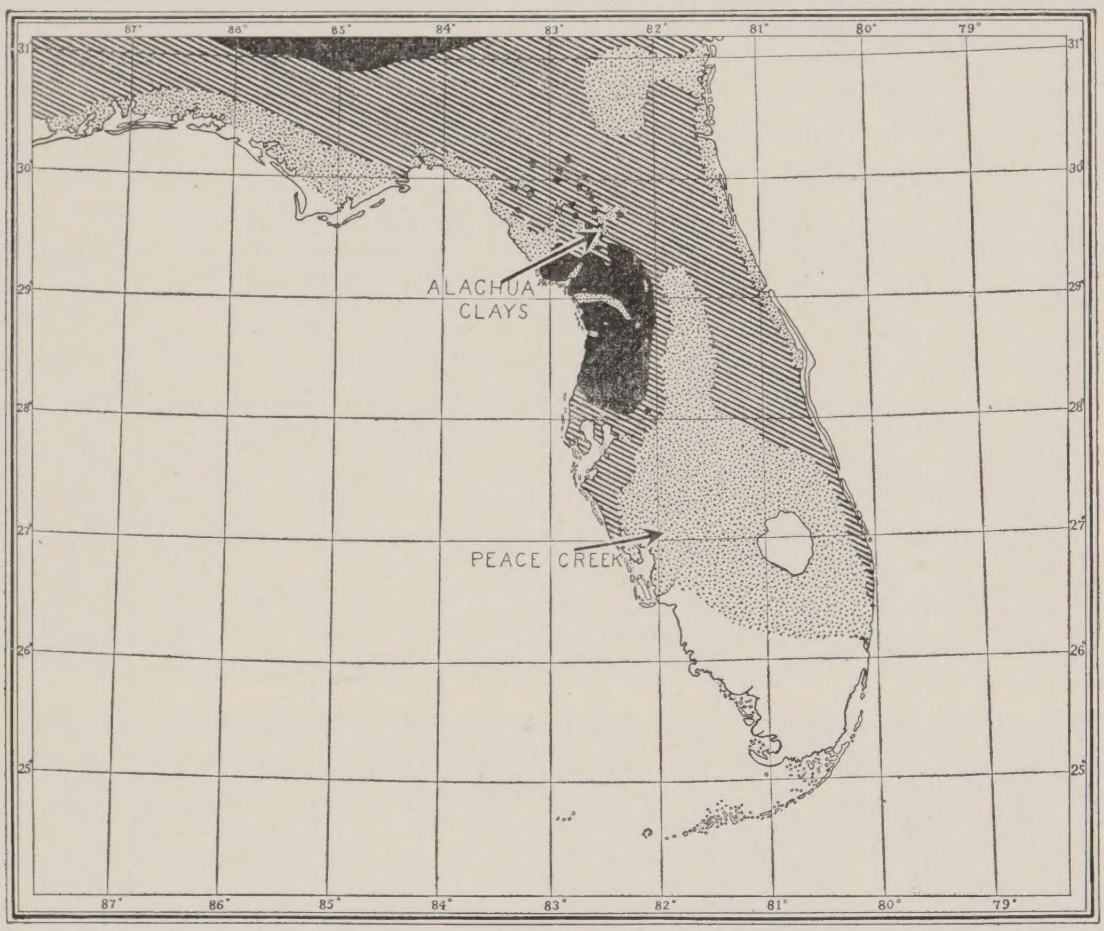


FIG. 160. — Geological map of Florida showing the area of distribution of the principal Cænozoic exposures and the location of the Alachua Clays (Lower Pliocene) and Peace Creek beds (Upper Pliocene or Pleistocene). Solid black = Eocene; ruled = Miocene; dotted = Pliocene; white = Pleistocene. After Dall, 1890.

these remains in the clays may be regarded as still a *desideratum*, we may be permitted to conclude with some confidence that at least they are not Miocene."

Among the first to notice the mammalian remains in these clays was Dr. Neal. They were first thoroughly examined by Dr. Joseph Leidy, who concluded that there were no species identical with those of the so-called 'Loup Fork' horizon of the West. But the more exact studies published in the names of Leidy and Lucas in 1896[2] led to the contrary opinion that these animals are in part specifically identical with those of the Republican River Formation of western Kansas. While this conclusion is based upon

[1] *Op. cit.* pp. 93, 133.

[2] Leidy, J. (Lucas, F. A. ed.), Fossil Vertebrates from the Alachua Clays of Florida. *Trans. Wagner Free Inst. Sci. Phila.*, Vol. IV, Jan., 1896.

rather imperfect specimens, very little doubt remains of the substantial similarity in the age of these faunas. We discover here especially the short-footed or teleocerine rhinoceroses of the species *T. fossiger*. There are also remains of a long-limbed, hornless rhinoceros (*Aphelops malacorhinus*). Mingled with these are found hipparions (*H. ingenuum*). The proboscideans, or mastodons, are represented by *M.* (*?Trilophodon*) *floridanus*, a species with long, narrow grinding teeth, somewhat akin in their proportions to those of *M. angustidens* of Europe. There are also remains of a number of camels, including a giant form provisionally referred to *Procamelus*, but possibly representing the giraffe camel *Alticamelus*. The deer family is represented by teeth provisionally referred to the Virginia deer *Odocoileus*, but probably representing an ancestral stage of this animal. The remains of a tapir and of a *Megatherium* are also attributed to this same zone (*op. cit.* p. x), but are probably of more recent age.

The above list of mammals is that recorded from a point ten miles east of Archer, hence these are also known as the 'Archer Beds.' The appearance of the bones suggests that the animals were mired and then scattered by predatory Carnivora. Ashes and burnt clay were found beneath some of the bones, but there is no sufficient evidence of human agency in this; the fire may have been due to lightning, a frequent occurrence in Florida at the present time. The longitudinal splitting of the long bones, sometimes observed, may be due to the penetration and growth of roots in the hollows of the bones rather than to the agency of man.

These details have been dwelt upon at some length because it seems that here we have a source of positive evidence as to the survival of the teleocerine rhinoceros fauna in the southern United States into Pliocene times.

A much newer or Upper Pliocene fauna is that mistakenly attributed to the Alachua Clays from Ocala, Marion County, Florida, a fauna containing *Elephas* (*E. ?columbi*), horses (*E. fraternus*), llamas (*Auchenia*), and saber-tooth tigers (*Machærodus*). This 'Ocala' fauna corresponds rather with that of the Upper Pliocene or Lower Pleistocene Peace Creek Formation of south central Florida. It may prove that this Florida fauna is 'homotaxial' rather than 'synchronous' with the Republican River and successive faunas of the Western plains region, which we shall now examine.

The 'Republican River' of Kansas. Peraceras Zone

Here we discover a very rich mammalian fauna resembling that of the Alachua Clays in the presence of the rhinoceroses *Teleoceras fossiger* and *Aphelops malacorhinus*, and also containing the very characteristic rhinoceros *Peraceras*, which is believed to be an acerathere, or hornless.

The typical deposits are 100 feet in thickness and extend along the Republican River of northwestern Kansas; they are part of the 'Loup Fork' as described by Cope and other authors.

The famous 'Long Island Quarry' of Phillips County, Kansas, belongs in the Republican River phase, and is said to be a river channel formation cut through the mass of the flood plain Republican River deposits. It was

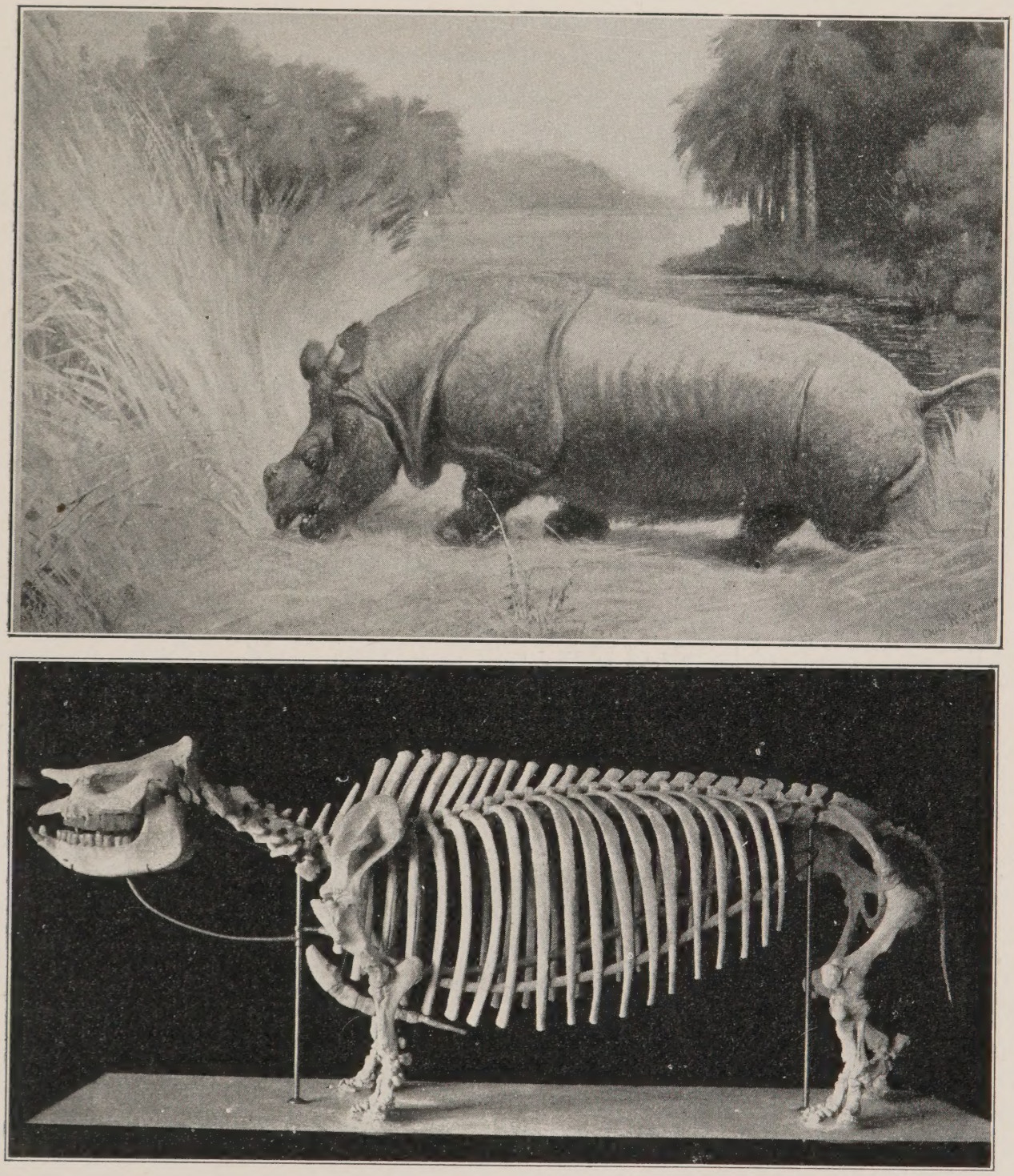


FIG. 161. — Old and New World short-limbed or teleocerine rhinoceroses of the Upper Miocene or Lower Pliocene. Above: Restoration of *Teleoceras*, represented in a Florida environment, from the original by Charles R. Knight. Below: Skeleton of *Teleoceras fossiger* from the 'Long Island Quarry,' Kansas. Both in the American Museum of Natural History.

discovered by Charles H. Sternberg as long ago as 1882, and has yielded remains of hundreds of teleocerine rhinoceroses of the species *Teleoceras fossiger*. It also contains species of *Ælurodon*, of *Pliohippus* (large), *Pliauchenia vera* (a small animal), of *Merycodus*, all animals characteristic of

the main mass of the 'Republican River' Formation. Several museums have secured materials of *Teleoceras* from this quarry sufficient to assemble the scattered bones into complete skeletons. The skeleton mounted in the American Museum of Natural History is shown in Fig. 161. The rhinoceros bones lie on the bottom layer of the 'Quarry,' mingled with sand about two feet in thickness; the heavy short bones of the feet and limbs lie at the very bottom; the skulls, arch bones, and vertebræ lie higher up. For this reason Sternberg is convinced that this was a quicksand deposit.

Some miles to the east is another locality in which remains of rhinoceroses and mastodons were found associated with those of large land tortoises (p. 342). As described by the last-named explorer, these tortoises were embedded together in a space 150 feet in length and some four feet in thickness; they were all found in normal position with plastron down, the heads and limbs attached. There is thus considerable evidence that this was part of a great assemblage of tortoises which had been overwhelmed by a sandstorm and died where they were entombed.[1] Another interpretation, by Hay, is that these reptiles had burrowed into the sand to hibernate; but this would hardly account for their facing in the same direction.

Characteristic Lower Pliocene Mammals

Multiple phyla of horses. — The Great Plains at this time were covered with great herds of horses of many different kinds. The browsing section is represented by *Hypohippus*, the last representative of the ancient anchitherine phylum of horses, with three toes and short-crowned teeth adapted to browsing. It is distinguished by nearly perfect transverse crests on the grinders, somewhat like those of early palæotheres.

The protohippine section as distinguished by Gidley[2] includes horses with three toes and long-crowned teeth, adapted to grazing; it subdivides into more primitive forms with subhypsodont teeth, such as *Merychippus*, and more progressive forms with long-crowned, well-cemented teeth, such as *Protohippus* and *Pliohippus*. The two latter animals are distinguished by the diverse characters of the preorbital fossæ on the sides of the face. In *Protohippus* these two fossæ are shallow, without sharply defined borders, while in *Pliohippus* there are two large and partly confluent fossæ, or depressions in front of the orbits, with sharply defined posterior borders. It is generally believed that the true horse (*Equus*) has descended from some more conservative or central forms, like *Protohippus*, but the species bridging the transition between *Protohippus* and *Equus* still await discovery.

A fourth and distinct line of Pliocene horses is that which contains the hipparions (*Neohipparion*), in which the antero-internal pillar of the premolars (protocone) is completely separated from the transverse crests.

[1] Sternberg, C. H., Letter.

[2] Gidley, J. W., Revision of the Miocene and Pliocene Equidæ of North America. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIII, Art. xxxv, Nov. 26, 1907, pp. 865–934.

These hipparions, in America at least, include the extreme desert-living types.

The American group of hipparions, or *Neohipparion*, differ from the hipparions of Europe and Asia in several characters: (1) the anterior pillar of the upper grinders is relatively larger and elliptical in cross section; (2) the enamel foldings are comparatively simple; (3) the limbs and feet, so far as known, indicate a more slender construction of the long bones and especially longer proportions of the metapodials. The skeleton of *N. whitneyi* (Fig. 123) was discovered by Mr. H. F. Wells of the American Museum expedition of 1902 in the Upper Miocene or Lower Pliocene deposits on Little White River near Rosebud Agency, South Dakota; the little cluster of animals was huddled together as if they had perished in a desert storm. It consisted of the superbly complete skeleton of an adult mare associated with incomplete skeletons of five other younger individuals undoubtedly of the same species. The age of this type (*N. whitneyi*) is quite probably Lower Pliocene.[1]

The increasingly arid conditions of climate were probably accompanied by an extension of the areas of the dry grassy plains and uplands over which these quadrupeds roamed, the hard conditions of the soil hastening the transformation from the tridactyl into the monodactyl condition.

Multiple phyla of rhinoceroses. — We have evidence also of the existence of four and possibly of five contemporary phyla of rhinoceroses.[2] As among the horses, surprisingly primitive persistent forms mingled with the most highly specialized. The polyphyletic character is also attributable to the intermingling of American and Eurasiatic strains. (1) The first phylum found among the aceratheres began with *Cœnopus persistens* in the Middle Miocene and is continued into the *C. brachyodus* of the Upper Miocene; the former species is slender, long-headed, with short-crowned teeth and primitive feet; the skull proportions are little changed from the Oligocene type; all these animals are small. (2) A second phylum includes a number of large, long-headed, long-limbed aceratheres with brachyodont teeth; these animals are closest to the Miocene aceratheres of Europe; they include the *A. ceratorhinus* and *A. montanus* found by Douglass in the Upper Miocene of Montana; the nasals are long and tapering and exhibit in the males a diminutive terminal horn. (3) A third phylum apparently, introduced by the *Aphelops megalodus* of the Middle Miocene, is mesaticephalic, with smooth nasals, with a high occiput inclined forward; it perhaps runs into the long-limbed *A. malacorhinus* of the Lower Pliocene. (4) Then comes a phylum of extremely broad-headed aceratheres, perhaps

[1] Gidley, J. W., A New Three-toed Horse. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX. Art. xiii, July 24, 1903, pp. 465–476.

[2] Osborn, H. F., New Miocene Rhinoceroses with Revision of Known Species. *Bull. Amer. Mus. Nat. Hist.*, Vol. XX, Art. xxvii, Sept. 24, 1904, pp. 307–326; also,

Douglass, E., Rhinoceroses from the Oligocene and Miocene Deposits of North Dakota, and Montana. *Ann. Carnegie Mus.*, Vol. IV, nos. 2 and 3, 1908, pp. 256–266.

introduced by *A. planiceps* of the Middle Miocene, and extending into the brachycephalic *Peraceras superciliosus* of the Lower Pliocene; in the latter animal the premaxillaries are weak and there are no superior canines; the hornless and pointed nasals resemble those of the aceratheres of Europe. (5) The most distinctively Old World form constitutes a fifth phylum; this is composed of the short-footed 'Teleocerine' (*Teleoceras*) rhinoceroses which now attain very large dimensions; the males are armed with horns placed at the very tip of the nasals; there is no evidence of the further evolution of the second or median frontal horn, which is observed in the Middle Miocene ancestor, *T. medicornutus;* although distributed over the entire northern hemisphere, these animals were clumsy, slow-moving, and resembled the hippopotamus in their proportions; it is not improbable that they largely frequented the sluggish rivers of the period.

Tapirs. — Tapirs still survive, but are very little known, being represented by the single species *Tapiravus rarus.*

Even-toed mammals. — The artiodactyls of the period include the surviving oreodonts, the browsing and grazing camels, the ancestral American cervids, the merycodonts, and the peccaries.

Among the camels, *Pliauchenia,* an animal characterized by the presence of only three premolars in the lower jaw, but in other respects showing much resemblance to *Procamelus,* is the most typical form. The Upper Miocene *Procamelus* is still present and abundant, and there are evidences in this formation of the existence of the giraffe or browsing camels (*Alticamelus*). The merycodonts are still represented by *Merycodus,* which, it will be recalled, is a delicately formed grazing type, with a skeleton analogous to that of the pronghorn antelopes, but with deciduous antlers of the American deer type.

The true American procervids are represented by *Blastomeryx,* an animal little known at this stage, but probably provided with simple, branched antlers. The peccaries are represented by *Prosthennops.*

Rodents. — Among the rodent fauna it is interesting to note the presence of *Eucastor,* closely related to if not identical with *Dipoïdes,* a rodent also observed in the Pliocene of Asia; it is possibly ancestral to the *Castoroïdes* of our Pleistocene, and it should be compared with the *Sigmogomphius* of the Pliocene of California. The peculiarly American family of Mylagaulidæ is now represented by *Mylagaulus,* a remarkable horned gopher (as discovered by Matthew), and by the still more specialized *Epigaulus.* These animals as a whole[1] seem to have been especially adapted to digging, for which habit they were far better equipped than any of the existing gophers. The highly modified feet and unusually small orbits suggest that they may have lived almost exclusively underground. Of what use could the horns have been to a burrowing rodent? They may prove to be sexual characters.

[1] Gidley, J. W., A New Horned Rodent from the Miocene of Kansas. *Proc. U.S. Nat. Mus.*, Vol. XXXII, June 29, 1907, pp. 627–636.

If not, it seems not improbable that they served as accessories to the great claws to assist in rapid digging.

The duplicidentate rodents are represented by the true hare (*Lepus*).

Lower Pliocene mastodons. — The giant forms of the period are the long-jawed, tetralophodont mastodons of the species *Tetralophodon campester* and *T. euhypodon*, both described by Cope. In the second species, *T. euhypodon*,[1] the symphysis of the jaw is abbreviated when we consider it in relation to the large size of the inferior tusks, yet it cannot properly be called 'brevirostral'; the superior tusks are compressed distally; the inferior tusks are large, cylindrical, and retain the enamel band. The other species, *T. campester*, embraces animals of larger size, with a very long symphysis in the lower jaw, *i.e.* of more primitive 'longirostral' proportions; the intermediate molars are tetralophodont, and the sixth molar has six cross rows of tubercles, and a heel.

Attention has been called above to the fact that the Lower Pliocene mastodons of Europe embrace both the trilophodont and tetralophodont types, and are believed to be short-jawed, or brevirostral, although this is not to the present writer's knowledge certainly known.

Carnivores. — The carnivorous enemies of this large herbivorous fauna are still very imperfectly known. Among the canids there are two species of *Ælurodon*. The *Ælurodon* was as large as the modern wolf, but had a short, heavy, mastiff-like head, and was distinguished from any living canids by the cat-like construction of the carnassial teeth. There is some, although not conclusive, evidence of the existence of an animal related to the bear-dog (*Dinocyon*) and known as *Borophagus*. The survival of these animals throughout the Pliocene of America as well as of Asia is rendered probable by the occurrence of *Dinocyon* limb fragments in the Middle Pliocene deposits (Blanco) of Texas. There is also some evidence of the existence of true dogs of the genus *Canis* from rare and fragmentary material.

Lower Pliocene, Late Phase

Snake Creek Formation (Ogallala) of Western Nebraska, Neotragocerus Zone

A more recent phase of the Lower Pliocene mammalian life of the region of western Nebraska has recently been revealed in the discovery by an American Museum party under Matthew and Cook[2] of the remains of a large and varied fauna, including no less than fifty species of mammals which are in many respects intermediate in evolution between those of the

[1] Cope, E. D., The Proboscidia. *Amer. Natural.*, Vol. XXIII, no. 268, April, 1889, pp. 191–211.

[2] Matthew, W. D., and Cook, H. J., Pliocene Fauna of Western Nebraska. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVI, no. 27, Sept., 1909, pp. 361–414.

'Republican River' stage above described and of the Middle Pliocene, 'Blanco' stage, of Texas.

The exposures in which this rich fauna occurs lie along a sand hill region, or crest of the divide between the Niobrara and Platte rivers in Nebraska, near the headwaters of Snake Creek, which gives the name to this formation. It is an outlyer of the 'Ogallala' of Darton, a formation which is typically composed of clean sand with a considerable amount of gravel; the Snake Creek is to be regarded as a local facies of the Ogallala. The bones occur

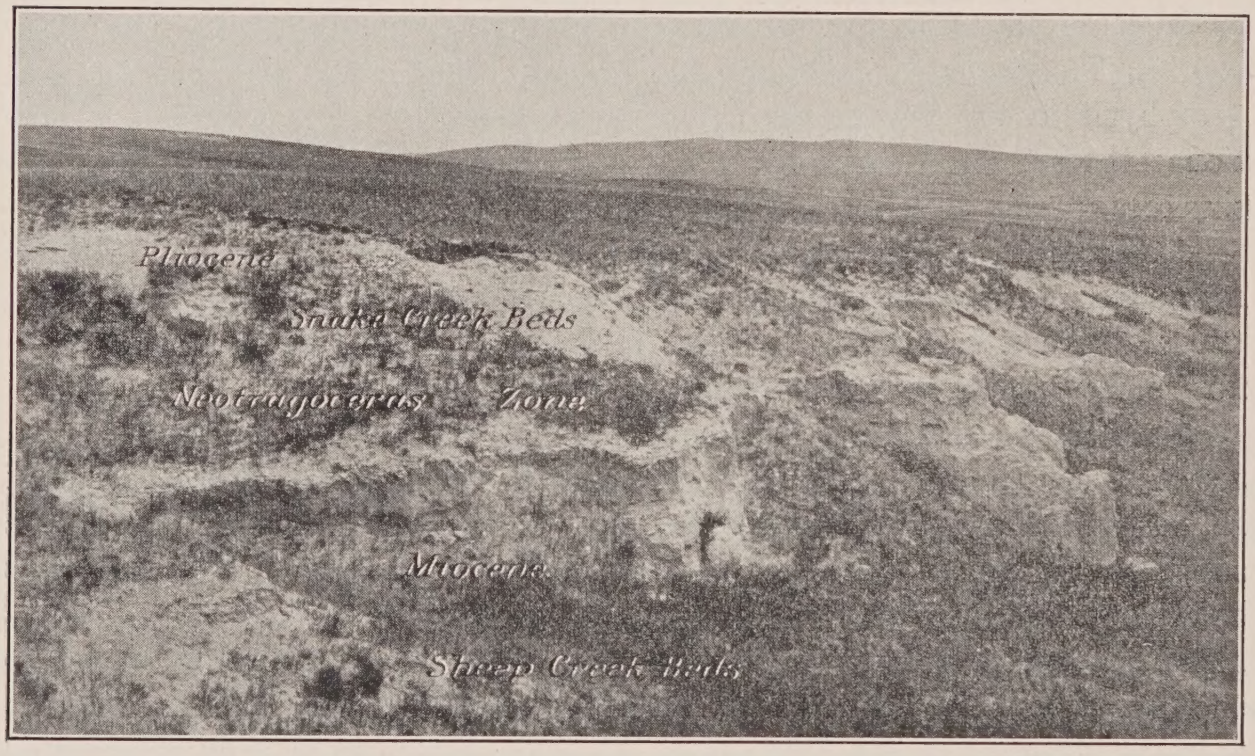


FIG. 162. — On the plains of western Nebraska. Miocene (Sheep Creek beds) overlaid by a Pliocene (Snake Creek) formation. Photograph by American Museum of Natural History expedition of 1908.

apparently in an old river channel, in such vast numbers as in places to form a veritable bone bed several feet thick, in which, owing to the scattering influence of river action, complete skulls and skeletons are very rare.

All the species and mutations are more advanced than those of the Republican River, or Peraceras Zone. Among the hoofed Herbivora all the Lower Pliocene types of rhinoceroses, however, still occur, including remains which are attributed to *Teleoceras*, *Aphelops*, and to a still simpler brachyodont rhinoceros probably belonging to the persistent brachyodont phylum mentioned under the Republican River (p. 348).

PREVAILING MAMMALS

Mastodons, longirostral
Tetralophodon
?Trilophodon (Florida)
Horses, several phyla

Among the dying-out members of the fauna are rare examples of the Miocene oreodont *Merychyus*.

The most important and unexpected feature of this assemblage is the evidence of the presence of the bovid division of the Cavicornia.

Rhinoceroses, 3–4 phyla
Teleocerine
Aceratherine
Peraceras
Aphelops
Aceratherium
Tapirs
Tapiravus
Gravigrade edentates
?Megalonychids
Last oreodonts, 2 phyla
Merycochœrus
Merychyus
Camels, llamas
Browsing camels
Alticamelus
Grazing camels
Procamelus
Pliauchenia
Cavicornia
Neotragocerus
Merycodonts
Merycodus
Pro-Cervids
Blastomeryx
Peccaries
Prosthennops
Carnivores
Rodents
Mylagaulids
(Horned gophers)
Primitive beavers
(*Eucastor, Dipoides?*)

For the first time in the history of the North American continent true antelopes are positively recognized, which appear to be related to the tragocerine, or flat-horned group,[1] characteristic of the European Miocene and Pliocene; hence the animal is named *Neotragocerus* and the zone in which it occurs the *Neotragocerus* Zone. The horn cores are perfectly straight, and of a round-oval section; they approach those of the existing mountain sheep (*Oreamnos*) but lack the curvature. The teeth and jaw of species of *Bison* also occur in this formation, but there is some doubt as to whether they are properly associated with this geological level, because the specimens may be intruders from a more recent formation.

Another possible newcomer is indicated by the presence of gravigrade edentates represented by an undetermined member of the *Megalonyx* family. It will be recalled, however, that the claw of a gravigrade edentate has been found in the Middle Miocene (Mascall) of Oregon, and there is a possibility that these giant sloths may have been resident in the forests of North America throughout the Cænozoic period, while not finding their way into the river and flood plain areas.

By far the most astonishing feature of the fauna is the extraordinary richness and variety of the horses; these are the most abundant animals in this formation. The four or five main phyla are the same as those in the Upper Miocene (p. 297), that is, we find remains of the conservative and presumably tridactyl browsing or forest horses (*Hypohippus* and *Parahippus*) intermingled with those of the intermediate stage in the evolution of the true horses (*Merychippus*). There are also several species belonging to the *Protohippus* and *Pliohippus* phyla, as well as several species of the desert-living horses (*Neohipparion*). This assemblage of conservative and progressive types of horses was certainly one of the most distinctive features of Lower Plio-

[1] In the tragocerine group the horn cores are laterally compressed, as in the goats (caprine section), but the grinders are short-crowned, resembling those in the brachyodont antelopes. (Flower and Lydekker, An Introduction to the Study of Mammals Living and Extinct, London, 1891, p. 349.)

cene times in North America. These animals must have swarmed in great herds over the prairies, the conservative or browsing types dwelling in the woodlands and copses. A marked approximation to the dental type of *Equus* is seen in certain varieties of *Neohipparion* found in this deposit, while certain varieties of *Pliohippus* approximate the South American Pleistocene horse *Hippidion*. There is no conclusive evidence that any of these horses were monodactyl, nor among the thousands of teeth preserved can a single one be referred to the genus *Equus*.

Among the camels the typical camel of the Upper Miocene (*Procamelus*) is well represented, as well as the giraffe camel (*Alticamelus*). Mingled with them are remains of gigantic pliauchenias, equaling in size and robustness those of the Middle Pliocene (Blanco Formation). The peccaries belong to the Upper Miocene genus *Prosthennops*, although the teeth begin to approach those of the Lower Pleistocene *Platygonus*. The remains of the American Cervicornia and of the merycodonts also present a mixture of Upper Miocene and of more recent character.

The rodents are again represented by the mylagaulids, or horned gophers, by the pocket gophers and primitive beavers. Among the latter we find *Dipoides*, an animal also observed in the Pliocene of China (Schlosser) and regarded by Matthew as possibly related to the *Castoroides* of the Pleistocene.

Among the carnivores are lions and saber-tooth tigers, amphicyons and cyons, ælurodons and true wolves (*Tephrocyon*), cacomistles (*Bassariscus*), and mustelids of several genera. (W. D. Matthew.)

Virgin Valley and Thousand Creek of Nevada

Reference has been made above (p. 338) to the astonishing discovery of strepsicerine antelopes or kudus in northwestern Nevada.[1] The sequence of the Tertiary formations in this region is as follows:

Terrace formations	Quaternary, late
Epoch of cañon-cutting (and of extensive faulting)	Quaternary, early
Deposition of Mesa Dolorite	Quaternary to Pliocene
Thousand Creek section	Pliocene to late Miocene
Virgin Valley Formation	Pliocene to early Miocene
Epoch of erosion and faulting	Miocene
Puebla Range series (=?Columbia Lava)	Miocene to Oligocene

The Virgin Valley Formation proper as explored by Merriam probably exceeds 1,500 feet in thickness; it is composed chiefly of volcanic ash and tuffs, the included gravels, sands, clays, lignitic and diatomaceous deposits being of much smaller volume than those of purely volcanic origin.

[1] Merriam, J. C., The Occurrence of Strepsicerine Antelopes in the Tertiary of Northwestern Nevada. *Univ. Cal. Publ., Bull. Dept. Geol.*, Vol. V, no. 22, pp. 319–330.

The mammal-bearing beds of the 'Thousand Creek' section seem to correspond mainly with the upper levels of the Virgin Valley. The fragmentary fossils found here are of extraordinary interest. The two large antelopes (*Ilingoceros, Sphenophalos*) exhibit close affinities to those of the tragelaphines of the Siwaliks of Asia, including the recent nilgai (*Boselaphus*), which in turn are related to the recent kudu (*Strepsiceros*), eland (*Oreas*), etc., of Africa. The kudu (*Strepsiceros*) and eland (*Oreas*) occur in the Siwaliks of southern Asia, as well as the nilgai.

Sphenophalos presents a near resemblance to the *Neotragocerus* discovered in the Snake Creek beds, Nebraska (p. 355), except in the comparative smoothness and denseness of the surface of the horn core, which suggests affinity to the recent prong-horn antelope (*Antilocapra*) of the Western plains. If this animal (*Sphenophalos*) proves to be intermediate between the bovine antelopes of Asia and our prong-horn antelopes, or antilocaprids, it will go to confirm the theory advocated by Matthew[1] that the American prong-horns are, after all, aberrant antelopes, that is, with affinities to the Bovidæ.

The true antelopes are represented by *Neotragocerus*, as well as by three species of the two Asiatic genera above mentioned.

A rich fauna of typical American mammals was contemporaneous with these antelopes in Nevada, and points to their Lower Pliocene age, especially in the survival of several species of rhinoceroses and the stage of horse evolution known as *Merychippus* and *Parahippus*. The forest-living horse (*Hypohippus*) and the desert-living type (*Neohipparion*) are somewhat doubtfully recorded. Among the aberrant Perissodactyla is a form attributed to *Chalicotherium*. The peccaries are represented by *Prosthennops;* the cameloids by *Procamelus* and *Alticamelus*. There is a species of *Palæomeryx* near *P. borealis*, as well as the deer-like antelope *Merycodus*.

The small fauna includes the sewellels (*Haplodontia*), marmots, hares, mylagaulids, castoroids (*Dipoides*), and gophers (*Geomys*); beside several kinds of canids there is a felid of gigantic size.

The Edentata are represented by remains of very large claws resembling those of the megalonychids except for a narrow median fissure.

Rattlesnake Formation of the John Day Valley, Oregon

As shown in the diagram (Fig. 164), this is the uppermost of the series of Cænozoic formations in the John Day region, overlying the Middle Miocene Mascall Formation and the Upper Oligocene John Day.[2] The type

[1] Matthew, W. D., A Complete Skeleton of *Merycodus*. *Bull. Amer. Mus. Nat. Hist.*, Vol. XX, 1904, pp. 101–129.

[2] Merriam, J. C., and Sinclair, W. J., Tertiary Faunas of the John Day Region. *Univ. Cal. Publ., Bull. Dept. Geol.*, Vol. V, no. 11, Oct., 1907, pp. 171–205.

specimens of the following species of Pliocene mammals are supposed to have been derived from the Rattlesnake beds:

Neohipparion occidentalis Leidy.
Neohipparion sinclairi Wortman.
?Platygonus rex Marsh.

To these should be added, from specimens in the University of California collection, a horse referred to *Pliohippus supremus* Leidy, also some remains of rhinoceroses which are specifically indeterminate, a large suilline form,

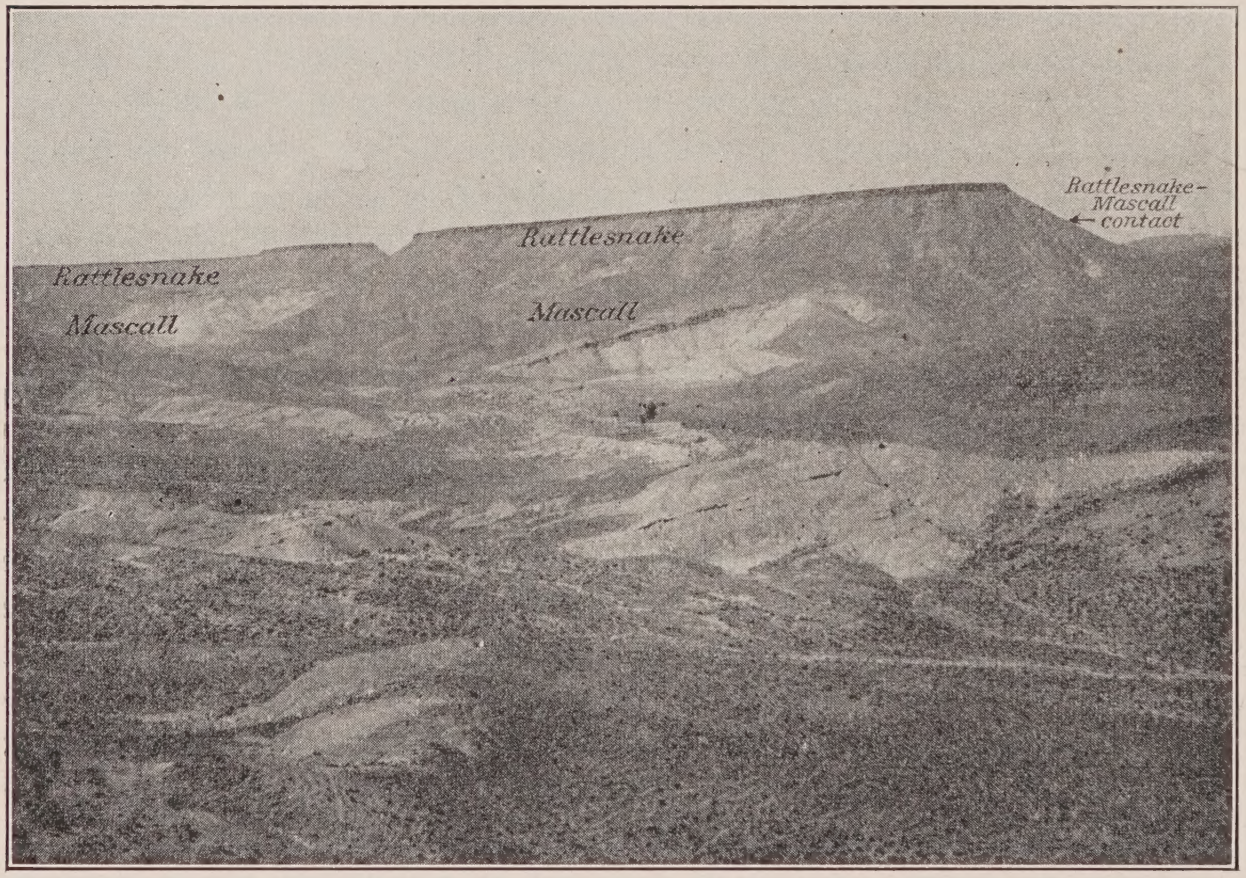
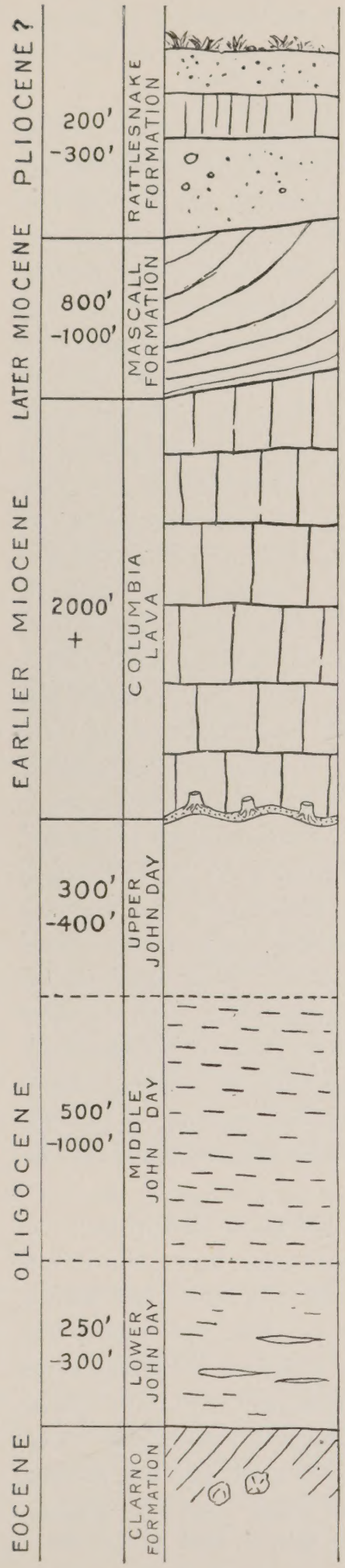


FIG. 163. — Miocene exposures near mouth of Rattlesnake Creek, John Day Basin, Oregon. Mascall formation (Middle Miocene) below. Rattlesnake formation (Lower Pliocene) above, separated by an unconformity. Photograph by J. C. Merriam.

fragmentary remains of a camel smaller than *Alticamelus*, and portions of a carapace and plastron of a land tortoise (*Clemmys hesperia*, Hay).

The Rattlesnake beds are composed of loose gravels, probably representing a fluviatile or flood plain deposition. These gravels, associated with tuffs and rhyolitic lavas, lie upon the up-tilted and eroded edges of the Middle Miocene Mascall Formation (see p. 288). The mammal remains have been obtained both from the tuffs and the gravels. The scattered and broken condition of the bones of one of the horses found in these beds also seems to indicate a long exposure of the remains on a land surface which was being rapidly worked over. The close of the Rattlesnake deposition marks the beginning of a long interval of erosion which may be regarded as the opening event of the Quaternary. (Merriam and Sinclair, *op. cit.*, p. 175.)



	Character	Remarks
Rattlesnake Formation, 200'–300'	Tuffs, gravels and lava (rhyolite) Average 150 feet	Few Fossils: Certainly from Rattlesnake: *Pliohippus supremus* (Leidy); Rhinoceros; Hog-like form; Small and large camel; *Clemmys hesperia* Hay; ? *Neohipparion*, *Platygonus rex*
	Unconformity	
Mascall Formation, 800'–1000'	Tuffs, tuff-shales, conglomerates	Mammalian fossils moderately abundant
Columbia Lava, 2000'+	Basalt with small amount of interstratified tuff	Separated from Upper John Day by surface of erosion on which trees grew. Trees were killed and buried by the lava. Heat of lava has baked Upper John Day to a brick red, but for a *few inches only* below the contact plane
	Brick red zone baked by heat of basalt	
Upper John Day, 300'–400'	Drab tuffs, becoming gravelly at top.	Camels in upper part of this division. Charred and silicified trees at contact with lava. These grew on an old surface eroded before extrusion of lava
Middle John Day, 500'–1000'	Greenish and drab tuffs, with many nodules Local rhyolite flows toward the top and bottom of this division	Abundant mammals Silicified tree trunks, standing erect, locally present
Lower John Day, 250'–300'	Red, green, and white tuffs and tuff-shales	*Elotherium* (large species) Rhinoceros (gen.? sp.?) Merycoidodont
Clarno Formation	Lavas, tuffs, tuff-shales and agglomerates Plant fossils exclusively	

FIG. 164. — Columnar section of the John Day Formation of Oregon, and superposed strata, Eocene to Pliocene. After Sinclair, 1909.

Middle Pliocene

Blanco Formation of Texas, Glyptotherium Zone

The Blanco Formation of Texas is decidedly distinct and more recent in its mammalian life than that of the Republican River, of the Rattlesnake, or of the Snake Creek beds, just described. It is provisionally regarded as of Middle Pliocene age. Its most distinctive characters are the appearance of short-jawed mastodons with few grinding teeth approaching the *Stegodon* type, and of South American armored edentates, or glyptodons.

Fig. 165. — Upper view of the shield and armored tail of *Glyptotherium* as exposed in the Blanco horizon of Texas. Photograph by American Museum of Natural History, 1900.

Cœnozoic beds of Texas. — Before describing the fauna of this very important formation, it is desirable to outline the characters of the Cænozoic deposits of northwestern Texas as successively studied by Cummins (1891) and Gidley (1899, 1900, 1901). As in Nebraska, South Dakota, Montana, and Oregon, we obtain vistas of the Cænozoic depositions in this southwestern portion of the United States which afford vivid pictures of the life succession. The credit for prior exploration belongs to Mr. W. F. Cummins of the Texas Geological Survey, whose early collections were submitted to Cope for determination. Credit for the more mature determination of the age of these beds and the fauna which they contain belongs to the American Museum expeditions conducted by Mr. Gidley. The following is a summary of the conclusions reached by the latter author.[1]

Since the close of the Triassic there has been no great disturbance or change of level in the region of the Staked Plains (see map), hence the strata of the Triassic which underly this hilly region are for the most part nearly horizontal, and the country at the beginning of the Miocene epoch was comparatively level. After a long period of erosion in which the Cretaceous deposits were removed during Lower or Middle Miocene times, flood plain and lacustrine conditions prevailed and the 'Panhandle Formation' (Fig. 167) was widely spread over the vast area now occupied by the Staked

[1] Gidley, J. W., The Freshwater Tertiary of Northwestern Texas. American Museum Expeditions, 1899–1901. *Bull. Amer. Mus. Nat. Hist.* Vol. XIX, Nov. 21, 1903, pp. 617–635.

Plains, extending westward to the Rocky Mountains of New Mexico, and spreading eastward over a much greater territory than they now occupy. All the formations succeeding the 'Panhandle' or of more recent date are

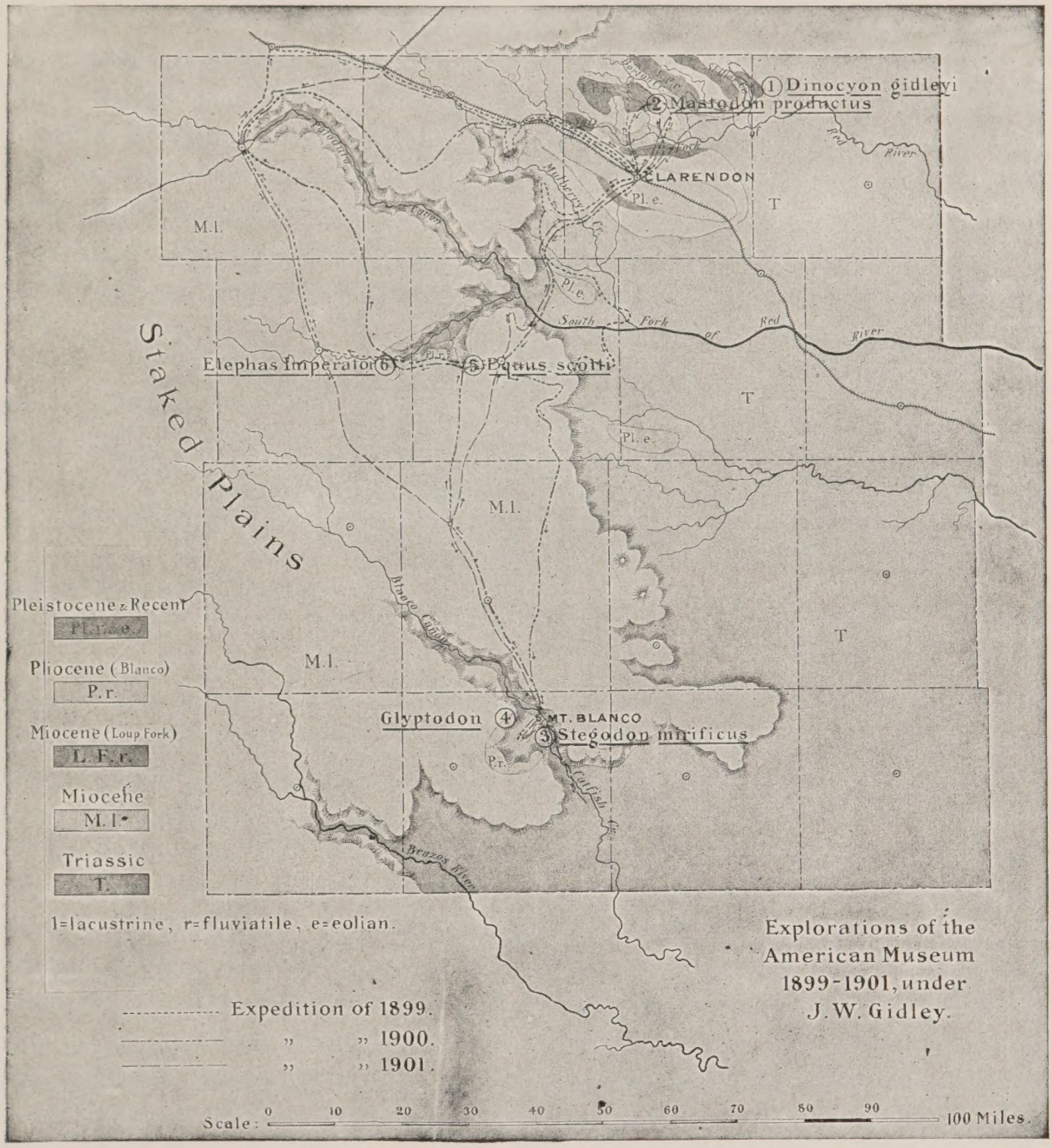


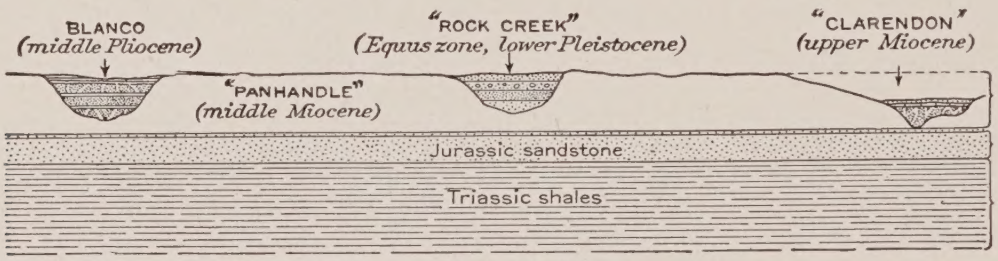
FIG. 166. — Map of a section of northern Texas showing location of important fossil mammal finds and geologic horizons. After Gidley, Amer. Mus. Exped., 1902.

represented by comparatively small areas of fluviatile, flood plain or æolian origin.

The earliest of these more restricted formations are known as the 'Clarendon,' and are of Upper Miocene or Lower Pliocene age, containing such characteristic forms as *Procamelus*, *Protohippus*, *Pliohippus*, *Hipparion*, and *Trilophodon*. The main body of the Clarendon beds consists for the most part of cross-bedded sands and sandstones, intermixing more or less

and cross-bedding with the clays; these indicate the existence of old river channels taking a nearly east and west direction, or approximately the same as that of the streams draining the country at the present time. Some of them are traceable for long distances. It is in these peculiar beds of sandy clays that all the fossils of this region occur.

Still more recent than these are new and fresh river channel formations (Fig. 167) which also cut their way into the Middle and Lower Miocene and constitute the famous 'Blanco Formation' of Cummins and Cope. These beds occupy a comparatively narrow valley or basin formed for their deposition by ancient erosion of the older Lower Miocene (Panhandle beds); they are traceable southeastward for fifteen or twenty miles to the edge of the plains; there is total absence of any proof for the theory



By permission of the American Museum of Natural History

FIG. 167. — Diagrammatic section of the Llano Estacado region of Texas, showing the intrusion of Miocene, Pliocene, and Pleistocene river channels in an older Middle Miocene Formation. After J. W. Gidley.

of lake origin of these beds, and many evidences of river or stream deposition. Occasional deposits of Fuller's or diatomaceous earth are accounted for by the supposition that there were in this ancient valley occasional pools filled with clear water partially isolated from the main stream. The animals which were preserved here include the armored and gravigrade edentates, the short-jawed mastodons, and advanced types of horses and camels.

A third period of river or flood-plain formation traversing the same Lower Miocene substratum occurred during the Pleistocene epoch, laying down the broad bands of the 'Rock Creek Formation,' also of fluviatile, alluvial, and æolian origin, composed of cross-bedded sands, gravels, and clays. The wind, carrying large quantities of fine dust and sand on the surrounding plains, may have played an important part in forming these deposits. The mammals represented consist wholly of land forms, and some of the bones show weather-checking; they contain the characteristic Lower Pleistocene forms, *Equus*, *Elephas imperator*, and *Platygonus*.

This geologic succession in Texas may be summarized as follows:

Lower Pleistocene, *Rock Creek Formation*	*Equus* and *Elephas imperator* Zone
Middle Pliocene, *Blanco Formation*	*Glyptotherium* Zone
Upper Miocene or Lower Pliocene, *Clarendon Formation*	*Procamelus* Zone
Middle and Lower Miocene, *Panhandle Formation*	*Merycochœrus* Zone

Mammals of the Blanco Formation. — The 'Blanco' of Texas takes its name from the little mountain of white sand near the edge of the Llano Estacado on Catfish Creek, which as a prominent landmark has been dignified by the name of Mt. Blanco. (Fig. 168).

The life phase of the Blanco is distinguished: (1) negatively by the undoubted extinction of the Oreodontidæ, a phylum which we have observed in its last stages in the Lower Pliocene; (2) by the apparent extinction of the rhinoceroses; in all the explorations which have been carried on in these beds no traces of these animals have been found; (3) by the apparent but not yet fully demonstrated absence of the forest or browsing horses of the *Hypohippus* type. No traces have been found either of the grazing horses with short-crowned teeth, or of the *Merychippus* type. Another browsing mammal which has not yet been found in this zone is the giraffe camel, or *Alticamelus*.

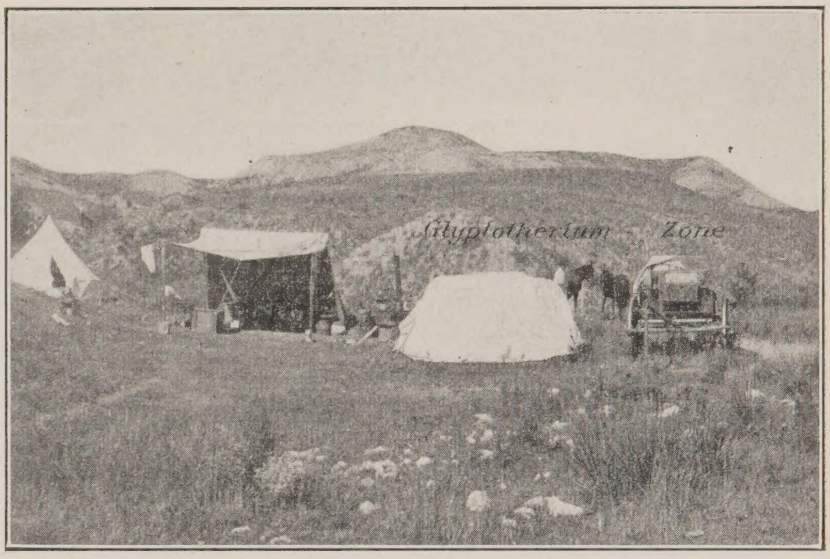


FIG. 168. — American Museum camp below Mt. Blanco, Crosby County, Texas. 'Mt. Blanco' is the white hill in the distance. Glyptotherium Zone. Photograph by American Museum of Natural History expedition of 1900.

Mastodons, brevirostral
?Tetralophodont
?Trilophodont
Stegodons
S. mirificus
Grazing horses, 3 phyla
Protohippus
Pliohippus
Neohipparion
Edentates
Gravigrades
Megalonychids?
Glyptotherium
Peccaries
Platygonus
Felidæ
Felis

Although the fauna is still imperfectly known, every branch of the mammals shows disappearances as well as certain new arrivals which are decidedly indicative of a new faunistic stage.

Of marked zoögeographic interest is the first appearance here of the giant glyptodonts, or armored edentates of South American type; it is of course impossible to determine whether these animals entered the country about this time or whether they had found their way there in the Lower Pliocene, because at no period do the glyptodonts extend very far north. Accompanying these armored edentates were the great hairy gravigrade sloths related to the genera *Megalonyx* and *Mylodon*, evidences of the existence of which we have already found in the Lower Pliocene and possibly in the Middle Miocene of North America.

In Texas and Nebraska, and probably in some

Mustelidæ
Canimartes
Canidæ
Canis
Amphicyonids

outlyers of the 'Ogallala Formation,' we find the first proofs of the existence in America of short-jawed or brevirostral Proboscidea. These mastodons as a rule have lower incisor teeth, and were hence termed *Dibelodon* by Cope; they possess many-crested molar teeth, in some respects resembling those of the *Stegodon* type.

Among the camels occur pliauchenias of very large size. The peccaries or dicotylids now pass from the Miocene *Prosthennops* stage into the Upper

FIG. 169. — Middle Pliocene mammals of Texas ($\times \frac{1}{30}$). Outline restorations by Charles R. Knight. *A*. The glyptodon *Glyptotherium texanum*. *B*. The giraffe-camel *Alticamelus*.

Pliocene and Lower Pleistocene *Platygonus* stage. This animal is a large, fleet-footed, or cursorial peccary, including two species,[1] the more primitive

[1] Gidley, J. W., On Two Species of *Platygonus* from the Pliocene of Texas. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX, July 24, 1903, pp. 477–481.

of which (*P. texanus*), it is interesting to note, presents a close relationship to the *P. rex* from the Rattlesnake Formation of Oregon.

The horses are imperfectly known, but it is certain that they still belonged to the three great grazing phyla *Pliohippus*, *Protohippus*, and *Neohipparion*, the browsing *Hypohippus* phylum having apparently disappeared, as well as the intermediate *Merychippus* phylum. One of the species of *Protohippus* (*P. cumminsii*) was so progressive in character as to have been referred by Cope to the genus *Equus*, but according to Gidley

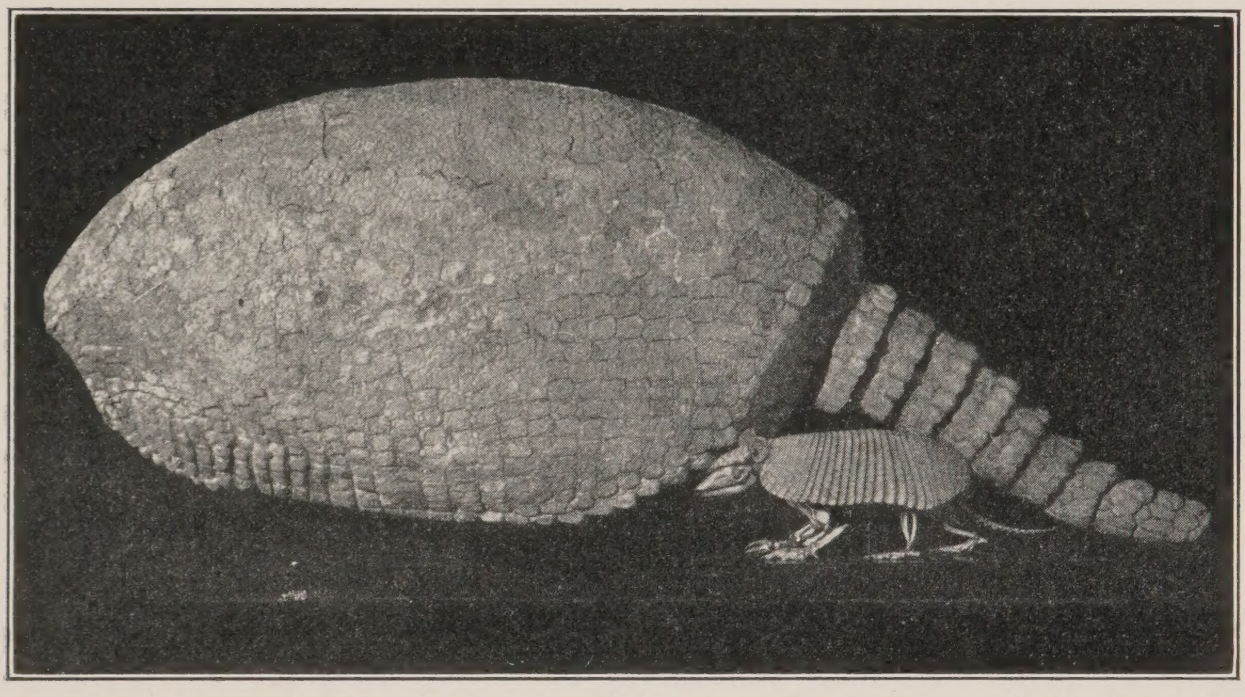


FIG. 170. — Carapace and tail of the Pliocene glyptodont *Glyptotherium* and skeleton of the recent armadillo *Xenurus*. In the American Museum of Natural History.

it shows a much closer relationship to the three-toed horse of the Miocene, though it is more advanced than any true Miocene species of this genus. The *Pliohippus* of this stage was also mistakenly referred by Cope to *Equus*, but its principal characters point to a more primitive phase than any true species of this genus.

Glyptodonts. — Among the edentates, *Glyptotherium* is the only one fully known. The existence of glyptodonts in Texas (1888) and Florida (1889) was first made known by Cope and Leidy. A fuller knowledge of these remarkable animals as they appear in the southern portion of the United States was revealed in 1900 by the discovery by the American Museum party under Gidley of a nearly complete carapace with tail armature of an animal found to be distinct from the South American glyptodonts and thus described as *Glyptotherium texanum* by Osborn.[1] This animal was very primitive and simple in its tail structure, which strongly suggests that of several of the Pliocene Santa Cruz types of Patagonia.

[1] Osborn, H. F., *Glyptotherium texanum.* A New Glyptodont, from the Lower Pleistocene of Texas. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX, Art. xvii, pp. 491–494, Aug. 17, 1903.

The general shape of the carapace is rather like that of the *Sclerocalyptus* than of *Glyptodon*. As in the Pampean *Panocthus*, the seventh to the fifteenth rows of lateral plates of the carapace are movable, or imbricating. Taken altogether this animal combines characters of several of the South American forms of the Miocene and Pleistocene periods.

The most important member of the Proboscidea is the *Mastodon* (*Stegodon*) *mirificus*, represented by a complete skull with the upper tusks preserved. This animal has been found in Nebraska, Idaho, and Texas. The upper tusks are round, without enamel, upturned, and divergent; the lower jaw is short and tuskless. In old age only four grinding teeth, the last upper and lower teeth on each side, are in use at one time. These third molars have five to six low cross crests, and are thus in a stegodon stage of evolution, but the crests are partly interrupted by supplementary median tubercles, so that it does not appear that this animal is closely related to any known species of the Asiatic *Stegodon*. A number of other species of mastodons were named by Cope from this formation from single molar teeth. It is thus uncertain whether they belonged to trilophodont or tetralophodont, long- or short-jawed series. The provisional references are *T. shepardi*, *T. tropicus*, *T. precursor*, *T. humboldti*.

Among the Carnivora a problematic feature is the earliest record of the genus *Felis* in the species *F. hillianus*, which may, however, be wrongly referred. The only musteline known is *Canimartes cumminsii*, an animal very remotely related to the marten, weasel, etc. The giant Carnivora of the period include the amphicyon-like *Borophagus*, also possibly a true species of *Amphicyon*.

Upper Pliocene or Lower Pleistocene

Equus and Elephas Zone

Considerable uncertainty again exists whether the formations here recorded should be arranged under the Upper Pliocene or under the Lower or initial stage of the Pleistocene.

The evidence afforded in Florida by the Peace Creek Formation is again singularly welcome, because we here find an *Equus* and *Elephas* fauna which is said to underlie marine beds of Upper Pliocene age. These geologic facts are so important in the chronology of American mammalian life that they may be described first.

Peace Creek Formation, Florida

There extends for miles along Peace Creek in Manatee County, southwestern Florida, a series of beds which Dall[1] has termed the *Peace Creek*

[1] Dall, W. H., and Harris, G. D., The Neocene of North America. *Bull. U.S. Geol. Surv.*, no. 84, 1892.

Formation. This author visited the Peace Creek region in January, 1891, hoping for an opportunity to observe an inter-stratification of marine beds with those containing mammalian remains. This anticipation proved to be well founded, because it produced the following results: the bone beds which are rich in the remains of mammalian life lie between an older marine Pliocene rock below and a newer marine Pliocene bed above, thus, in the opinion of this observer, determining its Pliocene character beyond question (*op. cit.* p. 133).

The mammals of these Peace Creek bone beds are much more recent than those of the Alachua Clays of Florida, although they do contain one type in common, namely, an hipparion (*H. ingenuum*). It will be recalled that *Hipparion* survives in the Upper Pliocene of Asia, also possibly in the Upper Pliocene of Europe,[1] and in the Lower Pleistocene of North Africa.[2] No teleocerine or other rhinoceroses appear in these Peace Creek bone beds. We notice also the absence of camels, which may be due, however, to local causes, because camels were probably flourishing at the same time on the Western plains and in California.

The mammalian assemblage, if found without association with Pliocene marine invertebrates, would certainly have been regarded as of early Pleistocene age rather than late Pliocene. We owe the description and identification of these remains to Leidy [3] in 1899, and they undoubtedly require revision to-day. It is possible

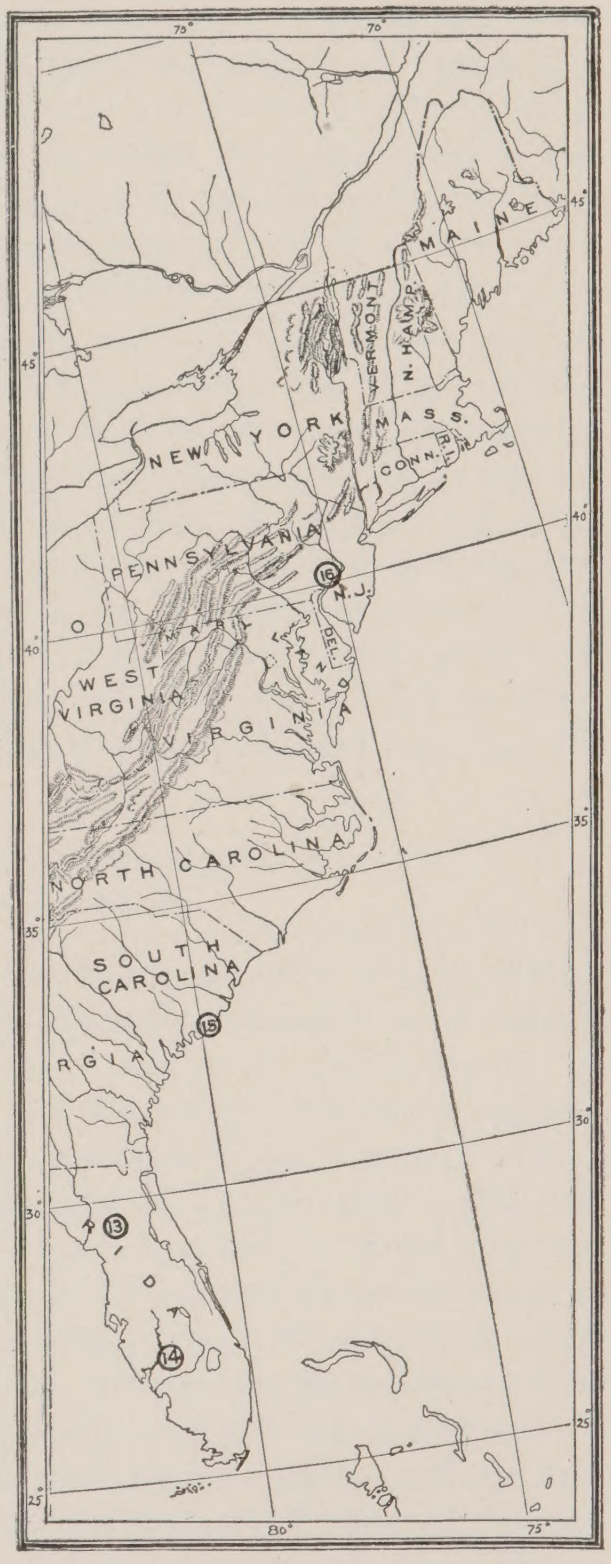


FIG. 171. — Chief fossil mammal deposits of eastern North America. **13.** Alachua Clays, Fla. **14.** Peace Creek, Fla. **15.** Charleston (Ashley River), S. C. **16.** Port Kennedy, Pa.

[1] Stehlin, H. G., Une Faune à Hipparion à Perrier. *Bull. Soc. Géol. France*, Ser. 4, Vol. IV, 1904.

[2] Pomel, A., Les Équidés. *Carte Géol. Algérie, Paléont. Monogr.*, Algiers, 1897.

[3] Leidy, J., Description of Vertebrate Remains from Peace Creek, Florida. *Trans. Wagner Free Inst. Sci. Phila.*, Vol. II, Dec., 1889, pp. 19–32.

that older and newer mammals are intermingled in these collections. The greatest anachronism is the reported occurrence of *Bison*. He states that the following fossils were collected in Peace Creek at Arcadia, Florida, from a sand bar which is exposed when the water is low: *Tapirus*, a tapir resembling the *T. americanus* of South America; a true horse, *Equus;* teeth and bones which may belong to some extinct species of *Hipparion*, a small three-toed equine; *Bison*, of the size of the recent American bison; a deer similar to the recent *Odocoileus;* a mammoth provisionally referred to *E. columbi;* among edentates, a glyptodont probably similar to *Glyptotherium*, also *Megalonyx*. The Sirenia appear in the manatee (*Manatus*). Among the reptiles there is a gigantic species of land tortoise (*Testudo crassiscutata*) as well as trionychids and emyids. Among the Proboscidea is recorded the true mastodon, *M. americanus*.

It seems hardly possible that this assemblage is all of the same age, and careful stratigraphic work and more accurate systematic determination of the species of mammals are necessary before the Upper Pliocene age of these forms can be considered as proved. The conclusion, however, seems well founded that we have here an *Equus, Elephas, Glyptotherium* fauna either of very late Pliocene or of early Pleistocene age.

'Loup River,' Nebraska, Formation, Elephas Imperator Zone

The same uncertainty applies as to the Upper Pliocene age of the original 'Loup River' formation described by Meek and Hayden in 1861–1862 in Nebraska, and to certain formations as yet unnamed in Texas and Mexico, which also contain remains of *Equus* and of *Elephas imperator*.

The typical 'Loup River' beds were first characterized by Meek and Hayden [1] as follows: "Fine loose sand with some layers of limestone — contains bones of *Canis, Felis, Castor, Equus, Mas odon, Testudo*, etc., some of which are scarcely distinguishable from living species." These sands lie on the Loup River or Loup Fork of the Platte River. Of the bones collected in this locality Leidy observed in 1869: "Other remains of elephants, as Dr. Hayden supposed them to be, he observed in association with those of *Mastodon mirificus, Equus excelsus*, and *Hipparion* at the head of the Loup Fork branch of the Platte River; also between this point and Niobrara River and on the latter." These species were determined by Leidy as follows: *Elephas imperator, Mastodon mirificus, Equus excelsus*.

The term *Loup River*, which was thus very loosely defined and circumscribed at the outset, together with the animals which it contained, although employed by Hayden in 1862 and 1869,[2] in 1871 and 1873, was,

[1] *Proc. Acad. Nat. Sci. Phila.*, Vol. XIII, 1861 (1862), p. 433. Also Leidy, J., Extinct Mammalian Fauna of Dakota and Nebraska, 1869, p. 255.

[2] See Leidy, *op. cit.*, 1869, Introduction.

with the animals which it contains, subsequently confused by both Hayden and Leidy themselves[1] with the very much older horizon of true Upper Miocene age as part of their Horizon F. 'Loup River' thus became identical in its loose significance with 'Loup Fork,' and the error spread into all subsequent literature.

It appears, therefore, that 'Loup River' was the original name applied to a fluviatile formation containing mammals solely of Upper Pliocene or Lower Pleistocene age, namely, *Equus* and *Elephas*.

Conclusions as to American Pliocene. — Few generalizations can be made from this scanty fauna and unsettled stratigraphy of the Pliocene. We are confronted with more gaps in our knowledge and with more unsolved problems than in any other epoch. Among the unsolved problems is the direct ancestry of the South American cameloids (*Auchenia*), the llamas, and guanacos, as well as of the true Old World camels (*Camelus*). We should discover here deer leading to the American type of deer (*Odocoileus*); we should also discover horses intermediate between the most progressive stages with tridactyl feet (*Protohippus*, *Pliohippus*) and the monodactyl *Equus*. It appears finally that while the Pliocene plains fauna is sparsely known, the Pliocene forest fauna is wholly unknown.

Causes of Pliocene Extinction

The disappearance of the browsing Herbivora and evolution of the grazing Herbivora, in the Great Plains region, we have observed as cumulative processes, beginning in Oligocene times (p. 240) and reaching a climax in the Pliocene.

Increasing aridity and prevailing summer droughts were characteristic of late Miocene and early Pliocene times in Europe, and evidence is accumulating that the same conditions prevailed in western North America.

Secular desiccation has been the fate of portions of three great continents in Pliocene and Pleistocene times, in each of which we observe a gradual modification and extinction of certain kinds of quadrupeds. These regions of increasing aridity are: (1) the Western plains region of North America, including the arid plateau and mountain region, beginning in Miocene times; (2) South America, Patagonia, and the Pampean region, beginning in late Pliocene times; (3) north central Africa, beginning in late Pleistocene times; (4) central Australia, beginning in Pleistocene times.[2]

Combining the facts brought together by many observers, Cope, Kowalevsky, Scott, Matthew, Hatcher, Stirling, we observe that the diminution of the softer kinds of vegetable food and increase of the harder kinds,

[1] See Leidy, *op. cit.*, 1869, pp. 15–21.

[2] Osborn, H. F., The Causes of Extinction of Mammalia. *Amer. Natural.*, Vol. XL, nos. 479 and 480, Nov. and Dec., 1906, pp. 769–795, 829–859. (See especially, pp. 783–787).

such as grasses, are accompanied by the extinction of a large number of the browsing Herbivora and by the rapid evolution of the grazing Herbivora, as was first thoroughly worked out in Kowalevsky's epoch-making memoir of 1873.

The influences of decreasing moisture are fivefold: (1) the character of the food supply changes with diminution of the softer and more succulent vegetation and increase of the harder and more resistant vegetation. (2) There is an increase in the length and severity of the dry seasons of the year. (3) Forest barriers are diminished or removed, and new competitors enter the country. (4) There is a reduction of the water supply and consequent elimination of the animals incapable of traveling long distances for food and water. (5) The evolution of grazing quadrupeds is favored, while that of browsing and forest-living quadrupeds is hindered. In brief, prevailing or increasing droughts entirely disturb the balance of nature; they compel migration; they expose quadrupeds to attack by carnivores by drawing them to restricted water pools; they favor quadrupeds able to dispense with a daily supply of water.

Facts of this kind enable us to understand the disappearance of the browsing horses, of the browsing chalicotheres, of the browsing and grazing rhinoceroses, incapable of traveling great distances, and of the browsing camels, and the evolution at the same time of the wide-ranging long-limbed types of grazing horses and grazing camels, which even in Pliocene times were probably acquiring the power of dispensing with daily draughts of water.

Influence of droughts. — Darwin describes [1] the devastating effects of the great drought in the pampas of South America between 1827 and 1830, during which great numbers of birds, wild animals, cattle, and horses perished from want of food and water. Cattle perished by thousands on the muddy banks of the Parana River. Similarly Azara describes horses perishing in large numbers in marshes, where driven in by thirst. In central Africa to-day the influence of gradual decrease of moisture is clearly illustrated in the conditions observed by such writers as Gregory.[2] The drinking places, or water pools, during long periods of drought become fewer in number and more widely separated, and large animals driven to them by thirst are more readily attacked and killed by Carnivora. Thirst, like hunger, drives quadrupeds to take extreme risks, which they would absolutely avoid during natural conditions of water supply. The pools become separated by distances of thirty to forty miles, thus necessitating long excursions to and from the various feeding places, during which quadrupeds are again exposed to attack. Finally, some of the pools dry up entirely, and, as observed by Gregory (*op. cit.*, p. 268): "Here and there

[1] Darwin, C., Journal. . . . Voyage of H. M. S. Beagle around the World, 1845. New ed., 1909, pp. 128–130.

[2] Gregory, J. W., The Great Rift Valley. 8vo, London, 1896.

around a water hole we found acres of ground white with the bones of rhinoceroses and zebra, gazelle and antelope, jackal and hyena . . . all the bones were there fresh and ungnawed. . . . These animals had crowded around the dwindling pools and fought for the last drops of water."

Such perishing of animals in great numbers from thirst would be one of many causes bringing about the condition of *diminished herds*, which may indirectly become a final cause of actual extinction through the inability of the enfeebled herd to protect its young.

Another effect of increasing desiccation is the increased number of alkali lakes, licks, and springs, and other areas of salt deposits. Alkali is sought by certain wild animals as a substitute for salt; the effects are not beneficial, and, as observed by Chestnut,[1] may predispose animals to the eating of noxious narcotic weeds.

We have, therefore, good grounds for believing that secular desiccation was one of the world-wide influences which caused the impoverishment of the magnificent fauna of early Pliocene times and the actual extinction of certain types of mammals.

[1] Chestnut, V. K., and Wilcox, E. V., The Stock-poisoning Plants of Montana: A Preliminary Report. *U.S. Dept. Agric., Div. of Botany, Bull.* 26, 1901.

CHAPTER VI

THE PLEISTOCENE OF EUROPE, NORTH AFRICA, AND NORTH AMERICA

We have seen that the Upper Tertiary or Pliocene closes with a world rich with life, a world replete with Asiatic and African influence. The Tertiary is followed by the Quaternary:

$$\text{CÆNOZOIC} = \begin{cases} \text{QUATERNARY} \\ \text{TERTIARY} \end{cases}$$

The grand divisions of the Quaternary in the New and Old Worlds are the same; namely, beginning with the Pleistocene and closing with the Holocene,

QUATERNARY

II. Holocene, or Recent. Mammals of prehistoric times. Domestication.

I. Pleistocene, or Glacial.

3. *Post-Glacial.* Mammals of existing species. Migrations and extinctions.

2. *Glacial.* Period of successive glacial advances and retreats. Mammals of extinct and existing species commingled.

1. *Preglacial.* Period of the incipient lowering of temperature and modification of animal and plant life.

In the Pleistocene period the fullness and precision of European investigation are in the strongest contrast to the preliminary results of American work, and in no other period may we anticipate more weighty inductions from correlation between the history of the Old and New Worlds. It is true that the Pleistocene history of Europe is still in a formative stage, but it is absolutely clear that a final and positive time scale and subdivision of the early Age of Man are not far distant, and that the vast labors of European geologists, botanists, zoölogists, palæontologists, and anthropologists will finally be rewarded with a harmonious theory of all the phenomena of the Quaternary epoch.

Combined attack by geological and biological methods has nowhere produced more brilliant results. The unaided testimony of the rocks and soils fails to tell us of the successive advances and retreats of the ice; but where, owing to the obliteration of surface deposits, geology is in confusion, the traces of plant and animal life serve both biology and meteorology like vast thermometers of the past, actually recording within a few degrees

the repeated rise and fall of temperature. Man, first with his crude implements and then with his skeletal remains, enters amidst these extinct floras and faunas, and affords a new and very precise means of marking off the stages of geologic time.

Geographic changes. — Elevation, subsidence, reëlevation, is the sequence of Pleistocene geographic change. The beginning of the Pleistocene is remarkable for its broad land connections, and represents the last stage of that community of fauna which during Pliocene times distin-

FIG. 172. — **Pleistocene, or Ice Age.** A period of maximum total elevation facilitating free migrations and invasions of life, culminating in the Glacial epoch, and followed by a prolonged depression. Portions of northern Europe and the coasts of North America greatly depressed. Then a period of reëlevation. Rearranged after W. D. Matthew, 1908.

guished the entire region of Europe, Asia, and Africa. The central geographic feature of the Ice Age was the *continental elevation*, which increased the land areas and connections and shut off the warm ocean currents, serving to lower the temperature. During the second Interglacial Period there occurred extensive volcanic disturbances in central Europe, giving rise to the hot spring formations of Thuringia (Taubach, Weimar).

The *general and local subsidence* which was the chief feature of closing Pleistocene times served to cut off all the old continental connections which had been characteristic of the Tertiary. As to the sequence of this depression, Ireland first lost its land connection with Wales and then with Scotland, and Great Britain became faunally isolated. In the Mediterranean in mid-Pleistocene times (Pohlig) the land bridge across Gibraltar

to Africa, also that between Italy, Sicily, and Africa, was broken; Malta and the other Mediterranean islands became isolated. To the eastward the Mediterranean Sea extended into the Ægean region and cut off the old land connection between Greece and Asia Minor. During a period of depression the Black Sea, the Caspian, and the Sea of Aral formed the large single sheet of water known as the Hyrcanian Sea. In Asia similar depression and separation phenomena were in progress. The islands of the East Indies, Sumatra, and Java were cut off from the Malayan Peninsula. The separation of the Japanese and Philippine archipelagos probably occurred in post-Glacial times. Similarly New Guinea and Tasmania, originally part of the Australian continent, became isolated.

It is premature to attempt to correlate these depression phenomena with the life zones. Late in Pleistocene times to the far northeast the Behring Straits were reopened, and only after a long period of community and free intermigration of Holarctic life, the Nearctic region of North America was completely isolated from the Palæarctic region of Eurasia.

VII. SEVENTH FAUNAL PHASE — QUATERNARY. IN THE NORTHERN HEMISPHERE THE GLACIAL PERIOD. VERY GRADUAL EXTINCTION OR EXPULSION OF SOUTHERN TYPES OF AFRICAN, SOUTH ASIATIC, AND SOUTH AMERICAN ORIGIN. FIRST APPEARANCE IN CENTRAL EUROPE AND NORTH AMERICA OF THE CIRCUMPOLAR TUNDRA FAUNA. IN NORTH AMERICA EXTINCTION OF THE REMAINING LARGE ENDEMIC QUADRUPEDS. THIRD AND FINAL MODERNIZATION BY A EURASIATIC OR NORTHERN INVASION OF NEW HARDY, FOREST, MEADOW, AND MOUNTAIN, RUMINANTS AND CARNIVORES.

The Quaternary is a time of transition, of vast extinction through natural causes, as well as geographic redistribution of life. During this epoch man becomes the destroying angel, who nearly completes the havoc which nature has begun.

We thus enter a new Faunal Phase, the Seventh. When its transitions are complete, the world wears an entirely new and somewhat impoverished aspect. The north has banished all the chief southerly forms and established the five modern zoölogical regions of the Old and New Worlds, namely: Palæarctic, Nearctic, Oriental, Ethiopian, Neotropical.

Similar divisions of the Seventh Phase in the New and Old Worlds. — It is natural in the present review to compare on a grand scale the mammalian succession in the Quaternary epoch with those in the various Tertiary epochs. It will be remembered that both in the Miocene (p. 249) and Pliocene (p. 309) of Europe we have evidence of *two faunal periods*. Tested

by the same standards there is considerable, but not as yet conclusive, evidence that both in Europe and North America the Quaternary exhibits *three faunal periods* (I, II, III), the first of these subdividing into two, as follows:

Faunal Period I

First fauna. Temperate fauna of late pre-glacial and early interglacial times. Several surviving Pliocene types. Species mostly now extinct.

Second fauna. Rich temperate fauna of interglacial times. Intermingling of extinct and recent species. Large southern element.

Faunal Period II

Third fauna. Entrance of an arctic or circumpolar fauna in the last glacial stages. Arrival of new *northern* elements. Southern element greatly reduced. Many existing species.

Faunal Period III

Fourth fauna. The prehistoric mammals. All existing species. A north temperate fauna of modern forest and plains types.

The secular climatic conditions in America were broadly contemporaneous with those in Europe; it is thus natural to expect to discover a *broad similarity* in the faunal succession, and it may be said that this expectation is realized. Close similarity should not be anticipated, first because the animals at the close of the Pliocene in the two countries contain many different elements (Europe including south-Asiatic and African, and America including South American forms); second, because physiographic conditions in America were different. Below the southernmost ice limit of the United States was a vast land area, whereas in Europe the Mediterranean closely bordered the ice-clad regions on the south.

There is little doubt that in both countries these four faunas broadly correspond with the advance of Pleistocene or glacial time as follows:

Fourth fauna, post-glacial and modern conditions.
Third fauna, maximum glacial, arctic conditions.
Second fauna, mid-Pleistocene interglacial temperate conditions.
First fauna, early Pleistocene temperate conditions.

Time Divisions of the Quaternary

The fluctuations of climate and of the animal and plant life of the Pleistocene are so numerous, so widespread, and so profound that it seems best to introduce the subject by a review of the great time divisions, together with some discussion as to the period when we should consider that the Quaternary proper begins. The reader will observe at once that these time divisions are based on evidence of four kinds:

1. Geological: glacial deposits and erosions.
2. Botanical: plant deposits, alternation of northern, arctic, and temperate floras.
3. Palæozoölogical: evolution, migration, and extinction of animal life.
4. Archæological: human implements, stages of human culture, skeletal remains of man.

Geologists are agreed that there were several *glacial* advances, differing in duration and severity, alternating with *interglacial* warm periods during which the ice retreated and conditions of climate prevailed which in some

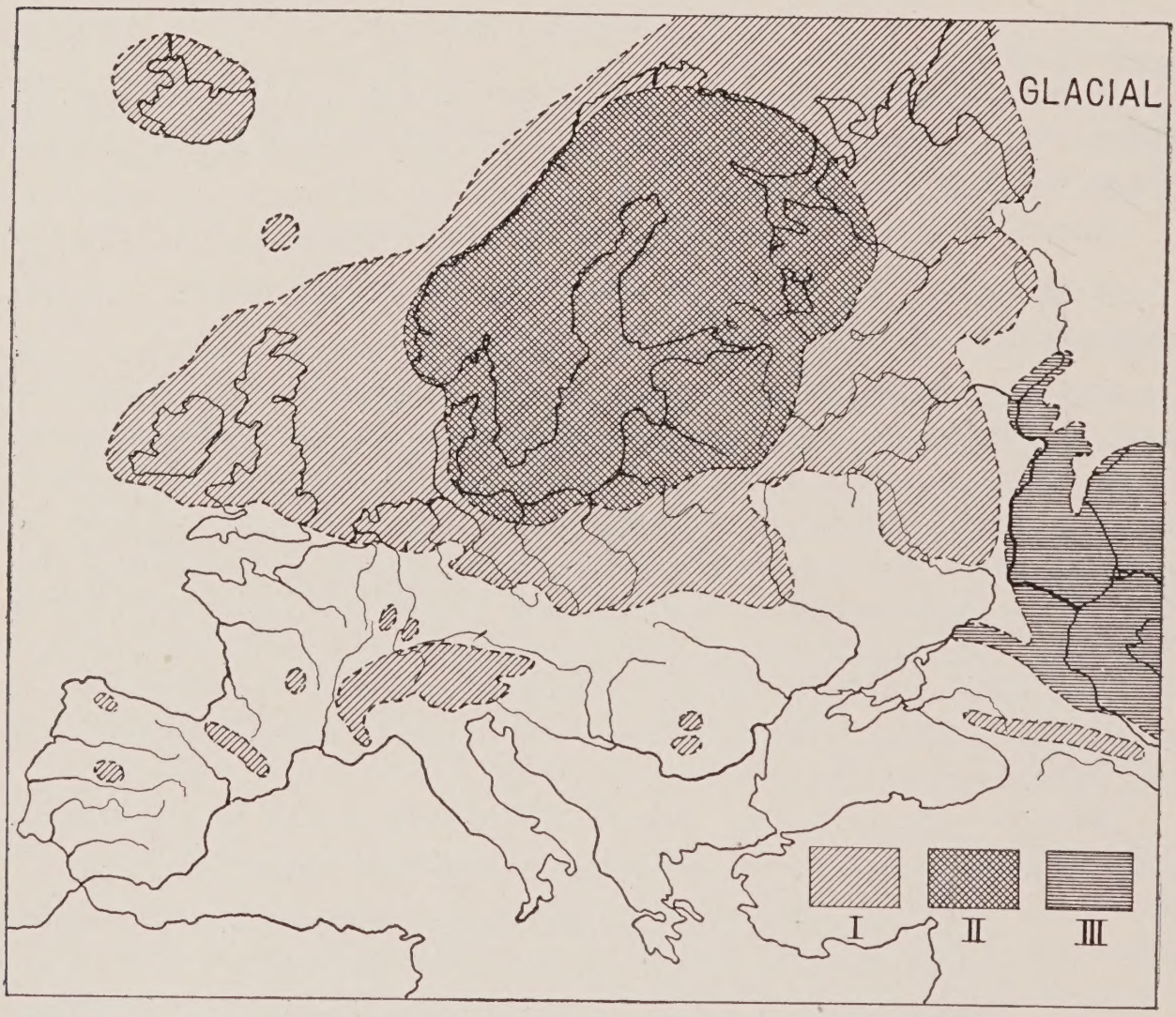


Fig. 173. — Europe in glacial times. I. Maximum glaciation. After de Lapparent, 1906.

instances were even milder than those of the same latitudes to-day. While in a sense rhythmic, both the glacial and interglacial periods differed in duration; they also differed in intensity in different parts of the northern hemisphere and as affected by the proximity of great mountain ranges or highlands on which the ice masses could accumulate. Thus near the Swiss Alps, Penck (1909) observes evidence of four great glacial advances and three interglacial epochs, while in northern Germany only three great glacial advances are recorded, because one of the series was not sufficiently extensive

to leave its records in regions so remote from the Alps. Similarly, American geologists have discovered evidence in certain parts of the United States of five great glacial advances, two of which are more or less confluent. It is obvious that in different parts of the northern hemisphere it will be easier to correlate the *first* and the *last* of these successive advances than to correlate the intermediate ones. The correlations which are suggested in the accompanying tables in square brackets [ ] are to be regarded, therefore, as in a large measure hypothetical.

Germany. — In studying the four faunal periods, we may first consider the divisions of the Pleistocene of northern Europe as discussed by Pohlig.[1] Pohlig introduces the Pleistocene with what he calls the Norfolk Interglacial Stage; this implies a previous glacial stage, in Great Britain at least (see p. 393). In strata of this age we discover what is generally regarded as the *First Pleistocene Fauna* and will be described as such in the present work. The mammals of the *First* and *Second* Pleistocene faunas are principally recorded in the warmer deposits of interglacial times, namely, the Norfolk, Skanian, and Helvetian. The times of the first, of the second, and perhaps of the third glacial advances have left no trace of mammalian remains in Germany; in the short arctic summers the districts left free by the ice were flooded by the melting of the glacial edges, and there was thus no chance for either plants or animals to exist. This does not appear to be true, however, of the final or fourth glacial time, namely, the Berolinian, which corresponds broadly with the last glaciations elsewhere, namely, with the Würm Glaciation of the Alps region or with the Wisconsin of North America. Here it is believed that we have records of animal life, or of the *Third Fauna* which existed during the period of advance, of maximum glaciation, and of retreat. The divisions of Pohlig appear to agree with those of Penck on this point, and would serve to explain the fact that preceding and *during the last glaciation we have our first positive records of the Arctic tundra and steppe types of mammals in Europe,* constituting the *Third Pleistocene Fauna.*

Switzerland. — The most recent results in Switzerland are those presented by Penck, which are shown, with some modifications, in the accompanying table.[2]

The Glacial Period in the Alpine Region

This table, which was prepared under Professor Penck's direction (March, 1909), brings out the two distinctive features of his theory, namely: (1) of the alternation of the Second and Third faunas; (2) of the correlation of the human culture stages with the interglacial periods. Both are important if sustained by sufficient evidence.

[1] Pohlig, H., Eiszeit und Urgeschichte des Menschen. Leipzig, 1907. These terms are used in a different order by James Geikie (1894). See also *Jour. of Geol.*, Vol. III, pp. 241–269.

[2] Penck, A., Das Alter des Menschengeschlechtes. *Zeitschr. Ethnol.*, no. 3, 1908, pp. 390–407.

Alternate migration theory. — The alternation is held by Penck to be demonstrated in Switzerland, where during the Riss Glaciation the *Third Fauna,* embracing the woolly mammoth (*E. primigenius*) and woolly rhinoceros (*D. tichorhinus*), first appears in Europe, only to be succeeded, however, in the short Riss-Würm interglacial period, by the rearrival of the *Second Fauna,* including the straight-tusked elephant (*E. antiquus*) and the broad-nosed rhinoceros (*D. merckii*). This Second Fauna is again driven out during the final Würm Glaciation by the woolly elephant and woolly rhinoceros of the *Third Fauna.*

Faunal, glacial, and culture stages. — The six culture subdivisions of the Palæolithic are those introduced by French archæologists, for in France these successive stages were first clearly distinguished, especially by the elder de Mortillet; several of them are now recognized in Belgium. It will be noted, secondly, that Penck traces the earliest palæolithic culture stage, namely, the Chellean, back into the heart of the Pleistocene as contemporaneous with the second fauna of the very long and warm interglacial period, known as the Helvetian, or Mindel-Riss; whereas Boule would place the Chellean in the final, short interglacial period, or Riss-Würm.

The mammals and culture stages, therefore, are correlated by Penck[1] with the great fluctuations of the northern waves of mammalian life as follows. The *Second Fauna* of the long, warm Helvetian, or Mindel-Riss interglacial stage is considered contemporaneous with the Chellean phase of human culture typified at Chelles, France (Fig. 176, 15). This second fauna was forced to migrate southward during the Riss Glaciation, which was of long duration and accompanied by a severe climate, favorable to the northern forms of woolly elephant and woolly rhinoceros, constituting the *Third Fauna.* As the Riss glacier receded there followed the relatively short Riss-Würm interglacial epoch, in which we discover the return of our *Second Fauna,* and the evolution of a higher stage of human culture, namely, the Mousterian, to which belong the men of Neandertal, Spy, Krapina, and the animal remains of Moustier, which gives the name to this stage. This Mousterian culture period was contemporary with the Riss Glaciation as well as with the succeeding Riss-Würm interglacial stage. As this stage is followed by the final, or Würm Glaciation, the arcto-alpine mammals of the *Third Fauna* again appear in Europe. In the meantime the Mousterian culture stage gives way successively to the Aurignacian, the Solutrian, and the Magdalenian, the latter representing the height of the Reindeer Period, when the Third or arctic fauna spread over Europe. After the Magdalenian culture stage, which closes the Palæolithic series, there is an interval which marks the retreat of the last glaciation before the introduction of the Neolithic culture and the appearance of the *Fourth Fauna.*

[1] Penck, A., Das Alter des Menschengeschlechtes. *Zeitschr. Ethnol.*, no. 3, 1908, pp. 390-407.

THE GLACIAL PERIOD IN THE ALPINE REGION

Modified after mss. of PENCK, 1909

[Interpellations by the present writer in square [ ] brackets]

GEOLOGIC TIME DIVISIONS	CHARACTERISTIC GEOLOGICAL DEPOSITS	GLACIAL AND INTERGLACIAL EPOCHS	FAUNA	HUMAN CULTURE STAGES (as correlated by Penck)		HUMAN SKELETAL REMAINS
HOLOCENE			**[Fourth Fauna]**		NEOLITHIC	
MID-PLEISTOCENE–GLACIAL	Schweizersbild near Schaffhausen Kesslerloch Cave	[IV] *GLACIATION-WÜRM* R[1]. M	**[Third Fauna]**	Magdalenian Solutrian	[PALÆOLITHIC]	REINDEER MAN
			Elephas primigenius Rhinoceros tichorhinus			
		A.	**[Second Fauna]**	Aurignacian		Mentone
	Wildkirchli Cave of Mt. Säntis Dürnten Wetzikon	Short 3d Interglacial Epoch Riss-Würm	Elephas antiquus Rhinoceros merckii Ursus spelæus	Mousterian		Spy, Krapina, Le Moustier
			[Third Fauna]			NEANDERTAL MAN
		[III] *GLACIATION-RISS* M	Elephas primigenius Rhinoceros tichorhinus			
			[Second Fauna]	Acheulian		
	Leffe in Val Gandino	2d Interglacial Epoch, very long and warm Mindel-Riss	Elephas antiquus Elephas meridionalis (last appearance)	Chellean		
		[II] *GLACIATION-MINDEL*	Hippopotamus, etc.			HEIDELBERG MAN
		1st Interglacial Epoch	**[First Fauna]**		[EOLITHIC]	
		[1] *GLACIATION-GÜNZ*	Machærodus Rhin. etruscus E. meridionalis Hippopotamus			
		Pre-Glacial Epoch	Typical Pleistocene invertebrates: Pupa muscorum, Succinea oblonga, Helix hispida			
	Strong unconformity	Elevation 500 meters				
PLIOCENE (Summit of)					[EOLITHIC]	

[1] R = Retreat
M = Maximum
A = Advance
} of Glaciation

Prof. Penck is disposed to correlate the European Glacial epochs with the American, as follows:

Würm = Wisconsin
Riss = Illinoian
Mindel = Kansan

It was formerly supposed that the transition from the Palæolithic to the Neolithic was abrupt, but some recent authorities (Rutot, MacCurdy) are inclined to favor a more gradual development theory; thus the Tardenoisian industry, representing the beginning of the Neolithic, may be considered as a transformation of the Magdalenian; furthermore, the art of polishing stone implements did not appear until the fourth epoch (Robenhausian) of the Neolithic. From the Neolithic period to the present time there has been no great deviation in climate or in fauna. Thus Neolithic man, who belonged to a different race with polished stone implements, first appeared in post-glacial times, or at the beginning of the Holocene or Recent Period.

Theory of Boule. — The French palæontologist and archæologist Marcellin Boule[1] believes that Penck errs both in his correlation of the glacial periods with human culture stages and in his view of the alternate migrations of the arctic or third fauna of mammals. He maintains that of the three great glacial advances, one falls in the Pliocene and two in the Pleistocene. He observes that if one holds with Penck that all the glacial epochs are Pleistocene, the conclusion naturally follows that the Pleistocene opened with a time of great glaciation; but there is more ground for believing that the first glacial epoch at least was of late Pliocene age, and since the Norfolk Forest Bed deposits are probably transitional between the Pliocene and Pleistocene, even the second glacial epoch would be placed at the close of the Pliocene period. The nomenclature is largely a matter of terms, but the questions of alternate migrations and geologic age of the human culture stages are both very important and far-reaching. The accompanying table exhibits the wide difference of opinion between these distinguished authorities as to the geologic age of the culture phases.

Geological Divisions of Penck	Palæolithic Archæological Divisions of			
	Penck[2]		Boule	
Post-Glacial	Magdalénien	PLEISTOCENE	Magdalénien Solutréen	PLIOCENE PLEISTOCENE
Würm Glaciation	"		Moustiérien	
Third interglacial epoch	Solutréen[2]		Chelléen	
Riss Glaciation	Moustiérien[2]		"	
Second interglacial epoch	Chelléen		"	
Mindel Glaciation	"		"	
First interglacial epoch	"		"	
Günz Glaciation	"		"	

[1] Boule, M., Observations sur un Silex Taillé du Jura et sur la Chronologie de M. Penck. *Anthropol.*, Vol. XIX, 1908.

[2] Cf., however, Penck's later views, as expressed in the table (p. 379).

Human culture stages. — Our review of the time divisions of the Quaternary naturally closes with that of the human culture periods, which are most clearly presented in the accompanying table by de Mortillet,[1] and below will be found brief outlines of the history of Palæolithic man and the appearance of man in North America (p. 494).

G. DE MORTILLET'S CLASSIFICATION OF 1898–1908, BASED ON THE EVOLUTION OF HUMAN IMPLEMENTS[2]

Geological Periods	Historic Divisions	Materials and Types of Implements		Culture Stages
Holocene or Recent	Historic	Iron	Merovingian	XV — Wabenian
			Roman	XIV — Champdolian
				XIII — Lugdunian
	Protohistoric		Gallic	XII — Marnian
				XI — Hallstattian
		Bronze	Tziganian	X — Larnaudian
				IX — Morgian
	Prehistoric	Stone	Neolithic	VIII — Robenhausian
Quaternary or Pleistocene			Palæolithic	VII — Magdalenian
				VI — Solutrian
				V — Mousterian
				IV — Acheulian
				III — Chellean
Tertiary			Eolithic	II — Puycournian
				I — Thenaysian

The Eolithic Stage.[3] — The rude flints known as eoliths, which precede the earliest palæoliths of the Chellean Stage, have been the subject of much

[1] De Mortillet, A., La Classification Palethnologique. Paris, 1908.

[2] From A. de Mortillet's La Classification Palethnologique, Paris, 1898–1908. This classification is that of the elder de Mortillet, and it is considerably modified by more recent discoveries.

[3] MacCurdy, G. G., The Eolithic Problem, Evidences of a Rude Industry Antedating the Paleolithic. *Amer. Anthrop.*, Vol. VII, no. 3, July–Sept., 1905, pp. 425–479.

controversy.[1] Flints thought by some to be the work of man were discovered by l'Abbé Bourgeois in 1867 in the Miocene of Thenay, Loire-et-Cher, and in 1877 Rames brought to notice flints from the Upper Miocene volcanic ash beds of Puy-Courny, Cantal, in central France, a formation of the same age as the Pikermi fauna. In 1892 Brown proposed the term 'eoliths,' to distinguish these supposed very primitive artifacts from the 'palæoliths' and 'neoliths' of Lubbock (Fig. 174).

These flints are very rough, but rude as they are, they generally show one part shaped as if to hold in the hand, while the other part appears to be

Fig. 174. — *A*. Eolith, Mafflean Epoch, Belgium. *B*. Palæolith, Chellean Epoch, Milton Street, Kent, England. *C*. Neolith, Upper Robenhausian Epoch, Gille Leie, Denmark. Photograph by MacCurdy, 1909.

edged or pointed for cutting.[2] It is a puzzling fact that the earliest eoliths resemble the later ones, there being, therefore, little development or improvement in form for hundreds of thousands of years.

Eoliths have been discovered not only in Upper Miocene deposits of central France, but in early Pleistocene gravels of France (St. Prest) and Belgium, in southern England (possibly Kent), and in Upper Oligocene beds of Belgium. The Belgian geologist Rutot has devoted his life to the Eolithic period and proved that, like the Palæolithic, it is capable of subdivision into a number of stages or industries, which are geologically demonstrable (see Table by MacCurdy). Perhaps the most convincing discovery

[1] Wilson, J. H., Recent Journeys among Localities noted for the Discovery of Remains of Prehistoric Man. *Ann. N.Y. Acad. Sci.*, Vol. XVI, no. 2, Mar. 17, 1905 (read Jan. 18, 1904), pp. 65–74.

[2] Penck, A., The Antiquity of Man. Lecture before Washington Acad. Sci., Feb. 1, 1909. Abstr. *Science*, n.s., Vol. XXIX, no. 739, Feb. 26, 1909, pp. 359–360.

RELATIVE CHRONOLOGY OF THE EOLITHIC AND PALEOLITHIC OF THE STONE AGE (after MacCurdy)

Geological Periods			Glacial and Interglacial Epochs	Fauna	Human Remains	Cultural Epochs	Type Stations	
Quaternary	Upper	Flandrian	Daun Stage Gschnitz Stage Bühl Stage (Wisconsin)	Reindeer	Cro-Magnon, Grimaldi	Magdalenian	La Madeleine (Dordogne)	Paleolithic
						Solutréan	Solutré (Saône-et-Loire)	
				Bison				
		Brabantian	Würm Glacial		Grimaldi (Negroid), Combe-Capelle	Aurignacian	Aurignac (Haute-Garonne)	
				Equus caballus				
	Middle	Hesbayan	Riss-Würm Interglacial	*Ursus spelæus*	La Chapelle-aux-Saints, *H. Mousteriensis*, Spy, Krapina, Neandertal	Mousterian	Le Moustier (Dordogne)	
						Acheulian	Saint-Acheul (Somme)	
		Campinian	Riss Glacial (Illinolsan)	*Elephas primigenius* *Rhinoceros tichorhinus*		Chellean	Chelles (Seine-et-Marne)	
			Mindel-Riss Interglacial	*Rhinoceros merckii* *Elephas antiquus*		Strépyan	Strépy (Belgium)	
	Lower	Mosean				Mesvinian	Mesvin (Belgium)	Eolithic
					Homo heidelbergensis	Mafflean	Maffle (Belgium)	
			Mindel Glacial (Kansan)			Reutelian	Reutel (Belgium)	
Tertiary	Pliocene	Upper	Günz-Mindel Interglacial	*Elephas meridionalis*		Saint-Prestian	Saint-Prest (Eure-et-Loire)	
		Middle	Günz Glacial (Pre-Kansan)			Kentian	Kent (England)	
		Lower						
	Miocene	Upper		*Hipparion* *Dinotherium*		Cantalian	Puy-Courny (Cantal)	
		Middle						
		Lower						
	Oligocene	Upper						
		Middle				Fagnian	Hautes-Fagnes Boncelles (Belgium)	
		Lower						

of all is that recently reported of the presence of eoliths in the same deposits with a jaw of very low type (*Homo heidelbergensis*).

If they are to be regarded as human artifacts, the antiquity of man or of *a pre-human type given to shaping stone implements* is greatly increased: three or four times for the Pliocene, and six or eight times for those found in the Lower Miocene (Cantal). If, as claimed by Rutot, eoliths occur under strata of Upper Oligocene age, the length of time is still further

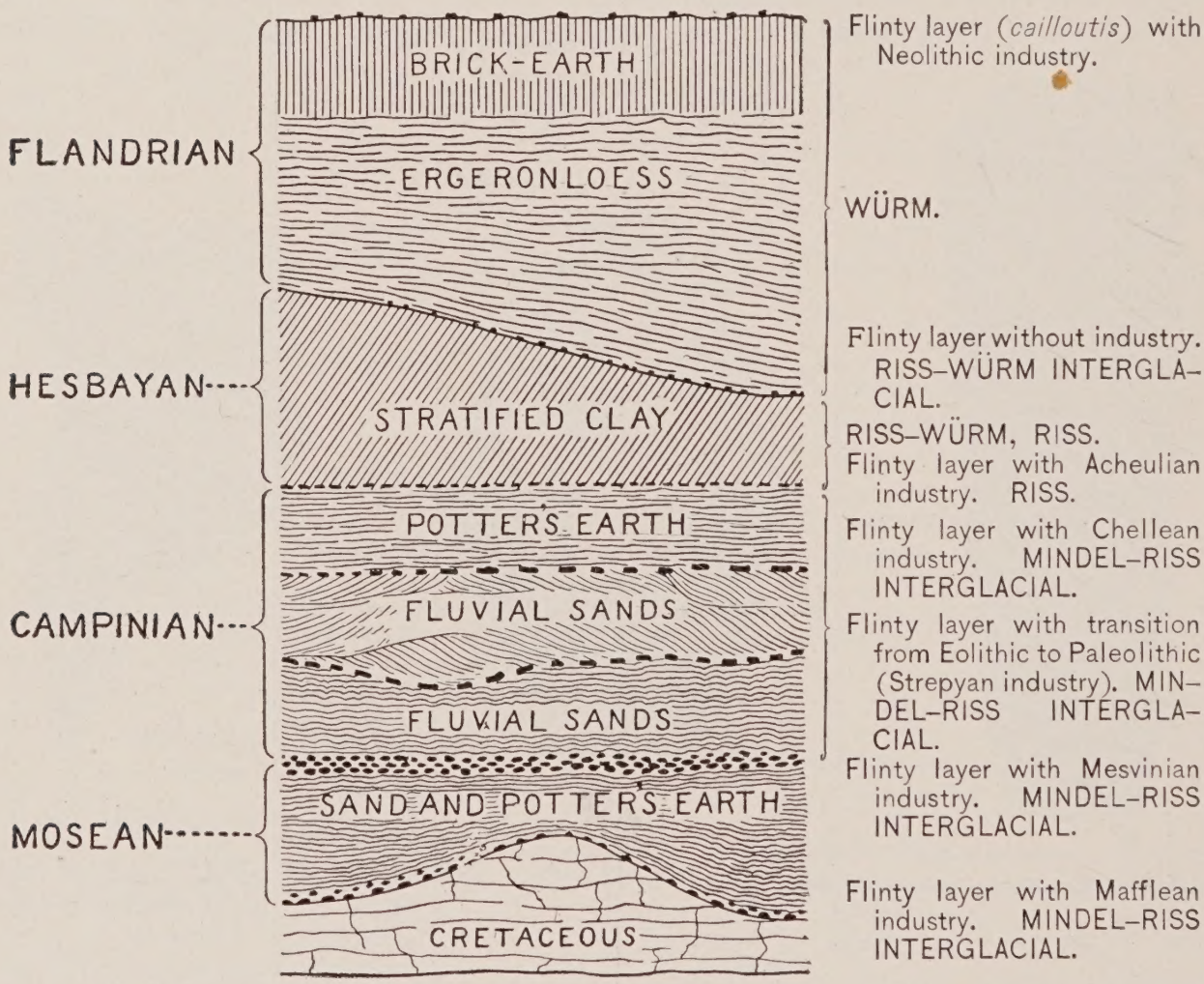


FIG. 175. — Section of the Exploitation Helin, near Spiennes, Belgium, showing the superposition of the Quaternary deposits; lower terrace of the valley of the Trouille. After MacCurdy, adapted from Rutot.

multiplied. The presence in the Miocene of France of extinct phyla of anthropomorphous primates offers one possible explanation of the origin of eoliths; it seems very unlikely, in view of their great antiquity, that any being at all closely resembling man (genus *Homo*) could have remained through such long ages while all other genera of mammals became transformed. The only known Miocene and Pliocene primate which might be considered as an 'eolith' maker is *Dryopithecus;* all others belong to existing phyla of monkeys, baboons, and apes. (Penck, 1909.)

The intermediate anthropoid, *Pithecanthropus*, attributed to the Pliocene by its discoverer Dubois in 1893, is now by Volz referred to the Pleistocene.

It is regarded by Schwalbe[1] either as a direct or indirect ancestor of the human phylum, standing intermediate between the apes and man in respect to its high brain capacity and the structure of its femur. It thus probably belongs in the family Hominidæ, and if so it had a grasping thumb.

Duration of the Pleistocene

The Pleistocene was estimated by Dana (1874) to be equal to one-fourth of the entire Cænozoic Era; by Ward (1885) and Williams (1895) it has been estimated at one-third of the entire Cænozoic Era. The tendency of more recent thought has been altogether in the direction of lengthening the duration of Pleistocene time. If with Wallace we accept Croll's theory and estimate, the last glacial advance would date back to the last period of great eccentricity, namely 200,000 years. The other figures show the variations of opinion on this subject and the increasing tendency to prolong the estimates of time.

Upham	1893	100,000 years
Sollas	1900	400,000 years
Penck	1908	500,000 to 1,000,000 years

The more recent estimates, although made by very high and usually conservative authorities, appear excessive unless we are to extend our estimates of Tertiary time (see p. 63) to twenty million years, and of pre-Tertiary time into hundreds of millions.

Penck has recently[2] (1908) pointed out the vast interest which attaches to this duration problem in connection with the antiquity of man. He believes that the whole Ice Age lasted somewhere between 500,000 and 1,000,000 years. The second, very long and warm interglacial epoch, known as the Helvetian or Mindel-Riss, is alone reckoned by him at several hundred thousand years, and the final short, or Riss-Würm, Interglacial Stage is reckoned at nearly 100,000 years. Since the climax of the final, or Würm, Glaciation he believes that from 30,000 to 50,000 years have elapsed. As regards the duration of palæolithic culture periods, the older palæolithic, or Chellean and Mousterian culture periods are of much longer duration than the newer palæolithic, or Solutrian and Magdalenian. Since the beginning of the latter, or Magdalenian, perhaps 24,000 years have elapsed; since its end perhaps 16,000. Compared with the Palæolithic divisions, the Neolithic stone and metal periods have occupied an almost unappreciable length of time; if the beginning of the age of metals dates back 3,000 to 3,500 years, that of the Neolithic lake dwellings began about 5,000 to 7,000 years ago.

[1] Schwalbe, G., Ueber fossile Primaten und ihre Bedeutung für die Vorgeschichte des Menschen. *Mitteil. Philomat. Ges. Elsass-Lothringen*, Vol. IV, no. 1, Decade 16 (1908), Strassburg, 1909.

[2] Penck, A., Das Alter des Menschengeschlechtes. *Zeitschr. Ethnol.*, no. 3, 1908, pp. 390–407.

Geologic deposits. — The chief geologic formations or deposits of glacial times are the following:

Glacial boulders, boulder clays, and drift.
Lignitic and swamp deposits.
Fluviatile gravels, till, and river terraces.
Lacustrine and marine terraces.
Loess, fine, calcareous, fluviatile and æolian loâm.
Volcanic travertines and tufas.
Phosphorites and other fissure deposits.
Cave deposits.

Loess, found in the Pleistocene of Europe, northern Asia, North America, and in the pampean regions of South America, is the most distinctive of all glacial deposits, next to the boulder clay and drift. It consists of a fine, porous, silicious and calcareous silt, usually of a light brown color, characterized by a peculiar competency to stand in vertical walls during erosion. Its distribution is quite independent of altitude, occurring in Europe from sea level to a height of 1,500 meters. Its origin is partly fluviatile, partly æolian. Thus it is believed that the fine mud carried by rivers becomes desiccated and is retransported by the wind. Penck (1904) describes loess as formed in districts traversed periodically by great streams, leaving dry mud which is redistributed by the wind. In Europe it is one of the most characteristic formations of the interglacial epochs; some loess deposits belong to the Riss-Würm Interglacial, others are known from the older Mindel-Riss Epoch, and some very rare deposits probably date back to the Günz-Mindel Interglacial epoch.[1] Another theory of formation is that the snow driven by the wind carried earthy material with it. Thus the loess remained as a residue after the melting of the snow.[2]

The plateau between Uzès and Avignon[3] contains numerous fissures filled with phosphorites which can scarcely be distinguished from those of Quercy but contain the remains of mammals of mid-Pleistocene age.

I. PLEISTOCENE LIFE OF EUROPE

Flora and Climate

It is clear from the great fluctuations of temperature and moisture which occurred during Pleistocene times that the flora cannot be treated as a unit nor as progressing in a single direction like the flora of the preceding

[1] Penck, A., Die alpinen Eiszeitbildungen und der prähistorische Mensch. *Arch. Anthropol.*, n.s., Vol. I, no. 8, 1904.

[2] Davidson, Charles, On Deposits from Snow Drifts with Especial Reference to the Origin of the Loess and the Preservation of Mammoth Remains. *Quart. Jour. Geol. Soc. London*, 1894, p. 472.

[3] Depéret, Sur les phosphorites quaternaires de la region de Uzès. *C. R. Acad. Sci. Paris*, Tome 120, 1895.

epochs. It presents alternations of arctic, boreal, and temperate species, which migrated southward and northward following the advances or retreats of the glacial cap. The broad divisions of the climate are as follows:

1. First cold phase, connected with the first glacial period.
2. The fairly warm climates of the interglacial periods.
3. The damp and cold climates of the last glacial advances.
4. The dry and cold climate of the period of the last glacial retreat in the age of the reindeer.

There is evidence both in Europe and North America that especially in certain of the long, warm interglacial intervals the climate in the northern hemisphere *was somewhat more equable and milder than at present, with a higher mean temperature and at certain intervals a greater precipitation of moisture.*[1] There was perhaps more sunshine than now. As a result of such favorable conditions arboreal vegetation flourished to the far north. The present tundras of Siberia and British America then supported forests which have long since been extirpated, the northern limit of similar living trees now lying far to the south.[2]

A picture of the flora of the very long and warm Mindel-Riss interval of the Second Interglacial epoch, the Chellean Stage of human culture according to Penck, in which the hippopotamus appears for the last time in northern Europe, is preserved in the *tuf de la Celle,* which contains remains of the sycamore maple (*Acer pseudoplatanus*), willows (*Salix*), the Austrian pine (*Pinus laricia*). Higher up in the same deposits we find the box tree (*Buxus*), not uncommonly the fig (*Ficus*); the sweet bay (*Laurus nobilis*) appears less frequently. In the upper part of the *tuf de la Celle* where Chellean palæoliths have been found, the fig and sweet bay are absent.[3] The climate was more damp and certainly milder than that of the present time in this region, the mean annual temperature being eight to nine degrees higher. In Lorraine below the level of the third Pleistocene fauna there occurs a flora in which the most northerly varieties of the larch (*Larix*) and the mountain pine (*Pinus lambertiana*) predominate. In still higher plant beds, the *tufs de Pont-à-Mousson* in eastern France, there are remains of forests composed of deciduous trees some of which have since migrated farther south. These are a few of the many instances showing the southward and northward migration of the flora in Pleistocene times, similar to those to be mentioned as occurring in the Toronto Formation of Canada (p. 448). There is strong ground for the belief[4] that there were cycles of climatic change beginning in earlier interglacial and succeeding glacial

[1] Croll, J., On Arctic Interglacial Periods. *Philos. Mag.*, Ser. 5, Vol. XIX, 1885, p. 36.

[2] Nathorst. Engler's Bot. Jahrb., 1881, p. 431; also Schröter, C., Die Flora der Eiszeit. Zürich, 1883.

[3] De Lapparent, A., Traité de Géologie. Paris, 1906, p. 1703.

[4] Penck, A., Die alpinen Eiszeitbildungen und der prähistorische Mensch. *Archiv. Anthropol.*, n.s., Vol. I, no. 8, 1904.

epochs. Since the mammalian life of the third and fourth glaciations (Riss, Würm), according to Penck, is identical in Switzerland at least, we may *ascribe tundra, or barren ground conditions, both to the fauna and flora of these final glacial epochs.* From the beginning of the last interglacial interval to the present time the vegetation of the region near the Alps has apparently gone through a cycle of changes such as the following:

Vegetation	Climate	Period
4th. Forest	West-European, oceanic	Modern
3d. Steppe	Southeast-European, continental	Post glacial
2d. Tundra	Northeast-European, sub-Arctic	Glacial
1st Forest	West-European, oceanic	Interglacial

The steppe and tundra biotic period, according to all authorities, was the great feature of the last glacial phases.

Neumayr estimated that the general lowering of temperature of Europe had not amounted to more than 6° C., and believes that even during the Ice Age a comparatively mild climate prevailed in Great Britain. Martins estimated that a lowering to the extent of 4° C. would bring the glaciers of Chamounix down to the level of the plain of Geneva. Penck estimates that, all other atmospheric conditions remaining the same as now, a fall of temperature to the extent of 4 to 5° C. would be sufficient to give us back the Glacial Period.

Secular Northward and Southward Migrations of Faunas

The passing from the Pliocene to the Pleistocene is clearly outlined on the east coast of England in Norfolk. After the first great cold wave the life of Great Britain is considerably altered; it constitutes the *first* fauna, as briefly defined above. This is followed in Europe by the *second*, by the *third*, and by the *fourth* faunas, as more clearly distinguished in the accompanying table, and explained above, p. 375.

The principal contributors to the theory of northward and southward migrations and to the succession of faunas are Nehring, Woldrich (1882), and more recently Penck. In considering the distribution and migration of the mammals throughout the Glacial Period, we must constantly keep in mind the differences of latitude. Italy had a more moderate climate than central Europe; the reindeer seems never to have found its way there, yet a lowering of temperature in Italy is indicated by the fact that the alpine mammals, such as the marmot (*Marmota*), chamois (*Rupicapra*), and steinbok (*Ibex*) came down to the plains.[1] The hippopotamus undoubtedly remained in Italy longer than it did in northern Europe, so it is not surprising to find its remains associated with those of the big-nosed rhinoceros (*D. merckii*) in a cave near Mentone in the French Riviera, which belongs in

[1] Issel, A., Liguria geologie e preistorica. Ref. by Boule in *L'Anthropol.*, 1893, pp. 602–604.

the period of Aurignacian culture, corresponding with the last glacial advance, according to Penck (see page 379). The same writer considers that at the time central Europe was tundra-like and Italy was a forested country.

I. Fauna. Mammals of the First, or Norfolk Interglacial Period	II. Fauna. Mammals of the Second and Third Interglacial Periods	III. Fauna. Mammals of the Last Interglacial, Glacial, and Glacial Retreat	IV. Fauna. Mammals, of the Prehistoric Forest, Meadow, and River Fauna of Europe
Climate temperate	Climate temperate to warm-temperate	Climate cold and dry	Climate similar to recent
The faunal zone of the last saber-tooths (*Machærodus*)	Hardy northern forms of African and south Asiatic mammals	First invasion of the arctic, tundra and steppe types, including numerous reindeer and musk oxen	Absence of rhinoceros and elephant, and extinction of the 'cave' animals
First appearance of the giant deer (*Megaceros*), of the musk ox, and of the bison South of the Alps the straight - tusked elephant and the hippopotamus	North of the Alps the straight - tusked elephant and the hippopotamus, the ancestor of the mammoth (*E. trogontherii*), and the broad-nosed rhinoceros (*D. merckii*) are abundant. The musk ox does not appear. Reindeer, if present, are rare.	The true mammoth, the woolly rhinoceros and the reindeer widespread in Europe	Rarity of reindeer
Eolithic implements	Eolithic and early Palæolithic man	The cave and loess periods of human culture Late Palæolithic man	Neolithic man

Penck[1] also observes that we cannot hope to trace a continuous evolution of forms during Pleistocene times, because we are not dealing with a development of one successive series in one locality, but with the cyclical alternation of a number of different faunas compelled to migrate through the alternations in the temperature and in the floras, the mammals disappearing and returning at intervals too brief to allow of any marked evolutionary changes. Herein lies our difficulty when we attempt to distinguish between the tundra faunas of the late glaciations and the forest faunas of the late interglacial epochs, because the faunas return not only with the same generic but the same specific types, as especially illustrated in the case of the mammoth (*E. primigenius*) and the giant deer (*Cervus megaceros*).

Implements of human manufacture, however, mark the progress of time because in the evolution of human culture the glacial epochs are separated by the successive advances in the fashioning of stone implements and in the primitive arts.

This 'alternate migration' theory is presented in the following table:[2]

[1] See Penck, A., Die alpinen Eiszeitbildungen und der prähistorische Mensch. *Arch. Anthropol.*, n.s., Vol. I, no. 8, 1904, p. 89, '04 in Bibliography.

[2] After Penck, 1904. The reader will observe some discrepancies between this table and that on p. 397.

Epoch	*Fauna*	*Vegetation*	(*Nehring*)	(*G. de Mortillet*)
Present	*Cervus elaphus*	Forest	Forest	Neolithic
4th, Würm, Glacial Epoch	*Elephas primigenius* *Rhinoceros tichorhinus* *Rangifer tarandus*	Tundra		Palæolithic Magdalenian Culture
Riss-Würm Interglacial (later part)	*Elephas primigenius* *Rhinoceros tichorhinus* *Equus caballus*	Grassy steppes	Steppe	Solutrian Culture
Riss-Würm Interglacial (earlier part)	*Elephas antiquus* *Rhinoceros merckii* *Cervus elaphus*	Forest		
3d, Riss, Glacial Epoch Maximum Glaciation	*Elephas primigenius* *Rhinoceros tichorhinus* *Rangifer tarandus*	Tundra	Tundra	Mousterian Culture

Rhinoceroses. — The three great rhinoceroses characteristic of the European Pleistocene, which probably belonged to two separate phyla, Asiatic, or Sumatran, and African, are of distinct geologic value. Of the former phylum, *D. etruscus* of the Val d'Arno [1] is a small animal of Pliocene and early Pleistocene times, distinguished by brachyodont or short-crowned grinding teeth, and long, slender limbs, two horns, the larger of which is posterior, and the absence of cutting, or front teeth; it is remotely related to the *Dicerorhinus*, or Sumatran phylum, but differs in the absence of cutting teeth. It belongs with the First Fauna, and does not survive into mid-Pleistocene times.

Succeeding this animal in early Pleistocene times both in Great Britain, France, and Italy, also surviving with the Second Fauna of the mid-Pleistocene of all Europe, is the broad-nosed rhinoceros, known as *D. megarhinus*, or *D. merckii*. It is distinguished from *D. etruscus* by long-crowned, or hypsodont grinding teeth; it resembles it in the smaller anterior and larger posterior horn, and in the elongation of its limbs and feet. In mid-Pleistocene times it became covered with hair, attained a great size, and was very abundant and characteristic.

The third species, the woolly rhinoceros (*D. antiquitatis*, *D. tichorhinus*), is, however, the distinctively cold weather, steppe, and tundra form, and belongs with the Third Fauna. Like the foregoing species, it has no front teeth, hence has been improperly considered as related to them, but it really belongs to the modern African group of *Atelodus* (*Diceros*), distinguished by a very large front horn and small posterior horn as in the existing "white rhinoceros" (*R. simus*).

The names of these three rhinoceroses are almost hopelessly confused in the early literature, though the characters were very clearly defined by Dawkins.[2] Both in the megarhine and tichorhine rhinoceroses and in old individuals of the Etruscan, the septum supporting the nasal bones becomes more or less fully ossified, to support the stout anterior horns.

[1] Dawkins, W. Boyd, On the Dentition of *Rhinoceros etruscus* Falc. *Quart. Journ. Geol. Soc.*, Vol. XXIV, 1868, pp. 207–218.

[2] Dawkins, W. Boyd, The British Pleistocene Mammalia, Pt. I, Introduction, 1866.

1. The First, or Early Pleistocene Fauna

As a whole the fauna of Europe is now distinguished from that of the Upper Pliocene by the *absence* of primates, mastodons, antelopes and gazelles, and tapirs.

This is the fauna of the first interglacial period, known as the Norfolk-Interglacial. It is typified in the Forest Bed of Cromer, Norfolk (Fig. 176,

Fig. 176.—**Pleistocene.** EUROPE.—**1** *Forest Bed of Cromer* (Norfolk). Sables de **2** *St. Prest* near Chartres (Eure-et-Loire). **3** *Malbattu* (Puy-de-Dôme). **4** *Peyrolles* (Bouches-du-Rhône). **5** *Solhilac* near Puy. Clay deposits of **6** *Durfort* (Gard). **7** *Cajarc* (Lot-et-Garonne). **8** *Val d'Arno* (Tuscany). **9** *Leffe* near Bergamo (Lombardy). **10** *Rixdorf* near Potsdam (Brandenburg). Gravels of **11** *Süssenborn* near Weimar. Sands of **12** *Mosbach* in northern Baden. Freshwater deposits of **13** *Clacton* (Essex). Sands of Mauer near **14** *Heidelberg* (western Germany). **15** *Chelles* on the Marne, near Paris. **16** *St. Acheul* (Somme). **17** *Ilford* and *Grays Thurrock* (Essex). Lignites of **18** *Dürnten* and of *Utznach*, near Zürich. **19** *Taubach* near Weimar. **20** *Wildkirchli cave* on *Mont Säntis* (eastern Switzerland). Tuffs of **21** the *Tiber Valley*, near Rome. Caves of **22** *Neandertal*, near Düsseldorf (western Germany), **23** *Spy*, near Amur (Belgium), **23a** *Krapina* (Croatia), **24** *Chapelle-aux-Saints* (Corrèze). Caves and alluvial deposits of **25** *Ternifine* (or *Palikao*) near Oran (Algeria), **26** *Pointe Pescade*, near Algiers (Algeria). **27** *Prince's Cave* (Monaco). Sandy clays of **28** *Vöklinshofen* (Alsace). **29** *Saalfeld* (Saxe-Meiningen). Travertines, etc., of **30** *Gera, Jena* (Saxe-Weimar). **31** *Leipzig* (Saxony). **32** *Solutré*, north of Lyons. Loess of **33** *Würzburg* (Bavaria). **34** *Thiede* near Braunschweig (Prussia). Cave of **35** *Montmaurin* (Haute-Garonne). **36** *Châteauneuf-sur-Charente* (Charente). Caves of **37** *Schweizersbild* near Schaffhausen, and *Kesslerloch* near Thayngen (northern Switzerland). Remains of lake dwellings at **38** *Wauwyl* (Lucerne), **39** *Robenhausen*, south of Lake Pfäffikon, **40** *Concise* on Lake Neuchâtel (Switzerland). Peatbogs of **41** *Hassleben*, near Weimar. Travertines of **42** *Langensalza* (Erfurt) in central Germany. Caves of the **43** *Island of Malta*, **44** *Island of Crete*, **45** *Island of Cyprus*.

1), in which certain mammals, such as the musk ox (*Ovibos*), are said (Dawkins) to occur, which are not found in more southerly localities. This

fauna has been treated as of Upper Pliocene age by some writers (Boule[1]); but since in the remarkably rich deposits of the Forest Bed of Norfolk, England, it *succeeds* a molluscan fauna of arctic affinity, there is little doubt that we are witnessing the mammalian life of the first temperate interglacial period. The chief localities in which this fauna occurs are the following:

Forest Bed of Cromer, Norfolk, England (Fig. 176, 1), typical of the northern life

Sables de St. Prest (Eure-et-Loir), France, (2) typical of the central life

Malbattu (Puy-de-Dôme), France, (3) typical of the central life

Peyrolles (Bouches-du-Rhône), France, (4) typical of the central life

Solhilac, near Puy, southern France, (5) typical of the central life

Durfort (Gard), southern France, (6) typical of the central life

Val d'Arno (upper deposits), northern Italy, (8) typical of the southern life

While many Pliocene animals have disappeared, the fauna still includes a number of forms *surviving* from the Pliocene, such as the saber-tooth cats (*Machœrodus*), the roe deer (*Capreolus*), the polycladine deer (*C. sedgwicki*), the more primitive dicerorhine rhinoceroses (*D. etruscus*), the horses (*Equus*), and especially the southern mammoths (*E. meridionalis*), and hippopotami. It is noteworthy that the saber-tooth cats and the polycladine deer do not reappear in the later Pleistocene formations of Europe, although the saber-tooths survive to a much later period both in Asia and in North America. No traces of the larger true, or leonine, cats (*Felis leo spelœa*) are recorded at this stage.

Among the *new arrivals* are the earliest and very numerous members of the giant fallow deer race, which terminate in the Upper Pleistocene in the giant deer *Megaceros*. The bison (*Bison*) certainly makes its first appearance in Europe, and according to some authors the true cattle (*Bos*) also appear at this stage. It is also important to note here the presence of a form (*Caprovis*) intermediate between the goat and the sheep, as the name indicates, most nearly resembling the mouflon of Sardinia. Among the rodents the large beaver (*Trogontherium*) succeeds the smaller species, first observed in the Pliocene of the Red Crag. South of the Alps the earliest of the straight-tusked elephants (*E. antiquus*) occurs. A giant hippopotamus (*H. major*) is certainly recorded, both south of the Alps and to the north in Great Britain. The greatest stranger among the new arrivals is the musk-ox (*Ovibos*), attributed by Dawkins[2] to the Forest Bed deposits.

Geologic proofs of the first glacial advance. — James Geikie[3] (p. 335)

[1] Cf., however, Boule, 1890, p. 945.

[2] Dawkins, W. Boyd, On the Alleged Existence of *Ovibos moschatus* in the Forest-bed, and on its Range in Space and Time. *Quart. Jour. Geol. Soc. London*, 1883, pp. 576–579.

[3] Geikie, J., The Great Ice Age and Its Relation to the Antiquity of Man, 3d ed., London, 1894.

favors the theory that the Forest Bed deposits were accumulated during an epoch of genial conditions which succeeded a colder glacial period in which the Chillesford and Weybourn Crags were deposited; these 'crags' mark the culmination of the cold conditions which began to manifest themselves as early as the Red Crag (p. 317) of Upper Pliocene times; at this culminating time the sea abounded in arctic molluscs. Even in the Red Crag, northern forms of molluscs begin to appear, and when we reach the Chillesford and Weybourn crags the marine molluscs present a decidedly arctic aspect. Immediately above the Weybourn Crag there is evidence of a climatic reaction, because the estuarine and fluviatile deposits of the Forest Bed contain a flora and a mammalian fauna of temperate type which contrast strongly with the assemblage of northern and arctic shells in the subjacent crag deposits.

Flora of the Norfolk Interglacial. — All the plants composing the Norfolk Interglacial flora belong to living species, and with a few exceptions are still indigenous to Norfolk, including such forms as the maple, hawthorn, elm, birch, alder, hornbeam, beech, pine, and spruce. The arrival of the spruce (*Abies*) is especially noteworthy because, although known in Miocene times in the arctic region of Grinnell Land, this is its first appearance in central Europe; it is also found in the interglacial lignites of Switzerland. It has since constituted an important member of the European forests. From this tree flora Reid concludes[1] that the climate was nearly the same as the climate of present times, but *slightly warmer*. This is in latitude 52° 40′.[2]

Contemporaneous with this temperate flora there flourished the remarkably rich mammalian fauna of the Forest Bed; the mammals also indicate conditions of climate somewhat warmer than those prevailing in the south of England to-day.

Mammals of the Norfolk Interglacial Epoch

For our knowledge of the mammalian life of the Forest Bed and contemporaneous fauna in France we are principally indebted to Dawkins (1880, 1883), to Newton (1880), to Gaudry (1893), to Boule (1902), and Pohlig (1907). Dawkins many years ago (1883, p. 579) gave the ratio of living, extinct, resident, and newly arriving mammals as follows:

Survivals from the Pliocene	11 species
Newcomers, extinct forms	6 "
" living "	21 "

The specific determinations of many of these animals, especially of the horses and the deer, await revision, and upon this closer study depend many

[1] Reid, C., and Reid, E. M., The Pre-Glacial Flora of Britain. *Jour. Linn. Soc., Botany*, Vol. XXXVIII, Jan., 1908, pp. 206–227.

[2] A list of these plants is given in Dawson's The Geological History of Plants, 1896, pp. 218–271.

interesting questions. The true red deer, or stag of Europe (*C. elaphus*), for example, was listed in this fauna by Dawkins, but Newton regarded it as very uncertain, and other authors consider that it first appears only in later Pleistocene times. The chief members of this mammalian assemblage are as follows:

Eolithic Man
(indicated by implements only)
Southern mammoths
E. meridionalis, (*?*) *E. trogontherii*
Straight-tusked mammoths
(in Italy only)
E. antiquus
Dicerorhine rhinoceroses
D. etruscus
Primitive horses
E. caballus fossilis
E. stenonis
Hippopotami
H. major
Polycladine deer
C. sedgwicki
Roe deer
C. capreolus
Axis deer (in Italy or
southern Europe only)
Giant fallow deer
C. dawkinsi, *C. verticornis*
(*?*) Musk oxen, or musk sheep
(in Great Britain)
(*?*) *Ovibos moschatus*
Bison
Bison bonasus
(*?*) Primitive true cattle
(*?*) *Bos primigenius*
Large beavers
Trogontherium
Saber-tooth cats
Machærodus (*?*) *cultridens*
Wolverines, or gluttons
(in Great Britain)
Gulo luscus

Forest Bed Fauna. — The authentic occurrence in the Forest Bed deposits of a number of mammals which are commonly attributed to this fauna was questioned by Newton[1] after very careful study of all the records and materials. It is certainly very important, now that we recognize a series of glacial and interglacial epochs, that mammals belonging to late Pleistocene times should not be attributed to the Forest Bed Interglacial Epoch without very conclusive testimony. Among the records which Newton considered *doubtful* are the hyæna, the broad-nosed rhinoceros (*D. megarhinus*), the true cattle (*Bos primigenius*), the red deer (*Cervus elaphus*), the moose (*Alces latifrons*), and the giant deer (*Megaceros*). The reference of the musk ox (*O. moschatus*) by Dawkins must also be considered somewhat doubtful.

Deer. — The presence of deer in great numbers and representing many different phyla is one of the most distinctive features of the times; it is certain that during the Norfolk Interglacial period there existed numerous and varied forms of deer life both in Great Britain and southern and western Europe. They belong to several, probably to as many as five, distinct phyla. The first of these, the polycladine, or 'many-branched' deer, so distinctive of the

[1] Newton, E. T., Notes on the Vertebrata of the Pre-Glacial Forest Bed Series of the East of England. *Geol. Mag.*, Vol. VII, Pl. XV, 1880, Pt. I, Carnivora, pp. 152–155, Pt. II, Carnivora, pp. 424–427, Pt. III, Ungulata, pp. 447–452.

Bear of the 'brown'
and of the 'cave' type
Ursus ferox, U. spelæus
Otters and martens
Wolves and foxes
Walrus (in Great Britain)
Trichecodon huxleyi

Upper Pliocene of the Val d'Arno, now make their last appearance in Europe as Sedgwick's deer (*C. sedgwicki*) of the Forest Bed, with wonderfully complex antlers, and closely related to the *C. dicranios* of the Val d'Arno. A second old European phylum is that of the roe deer (*C. capreolus*). A third phylum, numerous and highly diversified, is that of the giant fallow deer represented by a variety of species (*C. verticornis, C. fitchii, C. dawkinsi*). There is some doubt whether the true deer of the Carnutes (*C. carnutorum*) occurs here. The true fallow deer (*C. dama*) and the reindeer (*Rangifer tarandus*) certainly do not occur here. There is also some doubt as to the existence of the moose (*Alces latifrons*). As above noted, Newton is very uncertain as to whether the stag (*C. elaphus*) or red deer has ever been recorded in the Forest Bed. This animal certainly appears in the mid-Pleistocene in Europe and only at a very late stage in North America.

Surveying this Forest Bed fauna as a whole, we see that browsing, forest-living, and fluviatile types predominate. Among the carnivores are the wolverine, otter, two kinds of bear, wolf, fox, marten, a true feline (*Felis*) of doubtful reference beside the last representatives of the saber-tooth tigers. Among the forest-living browsers are the richly varied deer, a very large boar related to *Sus scrofa*, the browsing rhinoceros (*D. etruscus*) with short-crowned teeth; while in the rivers disported giant hippopotami (*H. major*).

Among the grazing and meadow-living forms either *Bison* or *Bos* is represented, more probably the former genus. There should also be included two species of horses, a heavier and a lighter form, the latter resembling the *E. stenonis cocchi* of the Val d'Arno. Estuarine conditions are represented by the presence of the walrus, the seal (*Phoca*), and of the cormorant (*Phalacrocorax*).

Lower Pleistocene of France. — The Lower Pleistocene deposits of France of approximately the same age as the Forest Bed are those of St. Prest[1] (near Chartres), of Durfort (Gard), of Solilhac (near Puy), and the recently discovered phosphorite deposits of Cajarc (Lot-et-Garonne) (Fig. 176, 7). These beds are placed in the Upper Pliocene by Boule, in the transition between the Pliocene and Pleistocene by Harlé and Stehlin, as well as by Depéret. Slightly more recent beds, the Lower Pleistocene age of which is not questioned, are those of Montsaune and Montmaurin (35) in the Pyrenees. Attributed to this age also are the plant beds of the forest of Moret[1] in the Seine valley near Fontainebleau.

[1] Dawkins, W. B., Early Man in Britain and his Place in the Tertiary Period. London, 1880.

We are disposed to consider all these deposits as of the same age as the Forest Bed and thus belonging to the first faunal zone or Lower Pleistocene. The mammals embrace substantially the same species, namely, the southern elephant (*E. meridionalis*), the Etruscan rhinoceros (*D. etruscus*), primitive species of horse, the giant hippopotamus (*H. major*), the large beaver (*Trogontherium*), and the bison (*B. bonasus*).

From Durfort was obtained the magnificent skeleton of a southern mammoth (*E. meridionalis*) described by Gaudry[1] (p. 397). The giant fallow deer are represented at St. Prest by the species *C. carnutorum* 'the deer of the Carnutes.' St. Prest is famous because in 1863 Desnoyer first discovered here the incised bones which are now considered as the work of Eolithic man.

The most recently discovered fauna of this age is that of Cajarc[2] in the northern part of the Rhone basin. Harlé and Stehlin consider it transitional between the St. Prest and Durfort and the Montmaurin deposits. The elephant (*E. meridionalis*) is of a type more recent than that typical of the Upper Pliocene. The *Bos* or *Bison* is of very large size. Especially interesting is the fact that these authors positively determine here relatives of the red deer (*Cervus elaphus*), leaving the specific reference doubtful. There is a large badger (*Meles taxus*) characteristic of the Early Pleistocene, a small wolf (*Canis*) no larger than a jackal. There is also a small species of saber-tooth tiger (*Machœrodus*).

In the cavern at Montmaurin in the Pyrenees[3] we have remains of an early Pleistocene fauna as different from that of the Upper Pliocene as it is from the Pleistocene cold fauna that followed it. According to Boule, it includes the broad-nosed rhinoceros (*D. merckii*), the red deer, or stag (*C. elaphus*), the roe deer (*C. capreolus*), as well as the saber-tooth tiger (*M. latidens*). The saber-tooth is certainly one of the most characteristic mammals of this Lower Pleistocene stage. In southern France, accompanying the southern mammoth appear the primitive Etruscan rhinoceros (*D. etruscus*) and the bison (*B. bonasus*). *Flora.* — Associated with the remains of these animals at Durfort[4] were those of numerous plants (*Planera, Parrotia, Quercus, Fagus*), of species now represented in the Caucasus, in Persia, in southern Italy, Portugal, and Japan. Again, in the interglacial forest of Moret (Seine valley) we find the fig (*Ficus*) and the Judas tree (*Cercis*), indicating a mild temperature. The tree flora, like that of Norfolk, thus indicates somewhat warmer conditions of temperature than prevail at the present time, the temperature of 4° to the south. Reid observes that the climate of this age was slightly warmer, but almost

[1] Gaudry, A., L'Éléphant de Durfort. Paris, 1893.

[2] Harlé, E., and Stehlin, H. G., Une Nouvelle Faune de Mammifères des Phosphorites du Quercy. *Bull. Soc. Géol. France*, Ser. 4, Vol. IX, 1909, pp. 39–52.

[3] Boule, M., La Cæverne à Ossements de Montmaurin (Haute-Garonne). *L'Anthropol.*, Vol. XIII, 1902.

[4] Gaudry, A., L'Éléphant de Durfort. Paris, 1893.

identical with the present.[1] The spruce forests (*Abies*) for the first time appear in Great Britain, in the Forest Bed. The most striking fact in examining the flora of the Norfolk and Suffolk coasts of England is its correspondence with the modern flora, in spite of the immense period of time that has elapsed and the great changes in climate during which all these plants were driven out and then permitted to return. "However," continues Reid, "though very similar, we find in the fossil flora several exotic species which give it a slightly different character, and we notice also the absence of several modern forms."

Characteristic Lower Pleistocene Mammals

This fauna as a whole is an outlier of the African, Asiatic group, with a strong northerly, or Eurasiatic, forest element intermingled. The reindeer is not present and the musk ox (*Ovibos*), if its presence be confirmed, is the only ruminant which can be said to give the Forest Bed a distinctively arctic character.

Elephants. — The southern elephant (*E. meridionalis*) of the times belongs to a somewhat more advanced type than that of the Upper Pliocene of the Val d'Arno. The Forest Bed specimens are, in fact, attributed by Pohlig[2] to the mid-Pleistocene species *E. trogontherii*. The southern elephant is best known from the magnificent specimen found at Durfort, France, and mounted under the direction of Gaudry in the Paris Museum; the height at the shoulders is 3.83 m., or 12 ft., $9\frac{1}{5}$ in. The following comparison of the relative heights of the great Pleistocene and recent elephants is based, so far as the extinct forms are concerned, on a series of approximations, because it is very difficult to measure the height of these animals from the skeleton.

	Estimated height at shoulder[3]		
	Feet	Inches	Meters
E. imperator, the imperial mammoth of North America	13	6	4.05
The straight-tusked elephant, *E. antiquus* of Europe			[4]
The southern elephant of Europe, *E. meridionalis*	12	9	3.83
The largest living African elephants, *E. africanus*	11	6	3.45
The Columbian mammoth of North America, *E. columbi*	11		3.30
The Indian elephant of Asia, *E. indicus*	10	6	3.15
The true or northern mammoth, *E. primigenius*	9	6	2.85
The living pigmy elephant of the Congo, *E. cyclotis pumilio*	7		2.10
The dwarfed elephant of Crete (*E. creticus*), Malta (*E. melitensis*), and Cyprus	5		1.50
The American mastodon, *Mastodon americanus*	9	6	2.85

[1] Reid, C., and Reid, E. M., The Pre-Glacial Flora of Britain. *Jour. Linn. Soc., Botany*, Vol. XXXVIII, Jan., 1908, pp. 206–227.

[2] Pohlig, Über *Elephas trogontherii* in England. *Monatsber. Deutsch. Geol. Ges.*, Vol. 61, 1909, no. 5, pp. 242–249.

[3] These figures are taken from Osborn, from Andrews' memoir, from estimates by F. A. Lucas, *Nature*, Sept. 10, 1908, from Pohlig (1907), and from Rowland Ward's Records of Big Game (8vo, London, 1907).

[4] See below.

The southern elephant[1] is Falconer's 'Preglacial variety of the mammoth'; it belongs to the same group as the true mammoth (*E. trogontherii, E. primigenius*) and the Columbian mammoth (*E. columbi*) of America. It is distinguished both from the African (*Loxodonta*) and from the Indian (*Euelephas*) types of elephants by its peculiarly flattened forehead and peaked cranium. It was taller than the true mammoth (*E. primigenius*) which only appears in late Pleistocene times. The tusks were shorter and less bent. We may infer from its original sub-tropical habitat that it was hairless. In tooth and skull structure it resembled *E. hysudricus* of the Siwaliks of India.

Two distinct stages of southern elephant are known, the more primitive of which has very low, broad teeth, with thick enamel. The other more progressive stage has dental plates of thinner enamel; this type occurs in the Forest Bed, at Durfort, and in the upper deposits of the Val d'Arno; it is said to be the original type of Nesti, who founded the species. There were thus two grand phyla of elephants evolving in northern and southern Europe at this time, the one (*E. meridionalis, E. trogontherii*) with remote resemblances to the Indian, the other (*E. antiquus*) with resemblances to the African elephants of recent times.

The straight-tusked elephant (*E. antiquus*) does not occur in the north at this time, but is found in the Arno valley of Italy, where it is associated with a fauna of almost tropical character, including the southern mammoth and the hippopotamus. The typical *E. antiquus* is recognized by its narrow, elongated grinding teeth with comparatively few plates,[2] which, combined with its skull characters, suggest its affinity to the modern African (*Loxodonta*) rather than to the Indian elephant (*Euelephas*) group. While in the first, or Norfolk, interglacial period it is confined to Italy, in subsequent interglacial times it wandered into northern Europe as one of the grandest and most distinctive forms, attaining a very wide distribution. Pohlig certainly overestimates its size[3] in assigning to it a height of 5 m. at the back (16 ft. 8 in.), or 1 m. more than the mammoth, and with tusks also 5 m. in length. In consequence of the size and weight of the tusks, the head, shoulders, and fore legs were enormously developed. The same writer believes that the habitat of this mammoth retreated and advanced with the successive ice waves and warm interglacial times.

The diminutive elephants of the Mediterranean islands were the dwarfed descendants of these straight-tusked elephants. The researches of Miss Bate[4] confirm the relationship to *E. antiquus* of these pigmy forms, which

[1] Pohlig, H., Eiszeit und Urgeschichte des Menschen. Leipzig, 1907, p. 120.

[2] Pohlig, H., Dentition und Kranologie des *Elephas antiquus* Falc. mit Beiträgen über *Elephas primigenius* Blum. and *Elephas meridionalis* Nesti. *Nov. Act. Ksl. Leop-Carol. Deutsch. Akad. Naturforscher*, Vol. LIII, no. 1. Halle, 1888.

[3] Pohlig, H., Eiszeit und Urgeschichte des Menschen. Leipzig, 1907.

[4] Bate, D. M. A., On Elephant Remains from Crete, with Description of *Elephas creticus sp. n. Proc. Zoöl. Soc. London*, Aug. 1, 1907, pp. 238–250.

attained a height of only 5 ft. She remarks that the adaptability to which *E. antiquus* owed its wide geographic distribution and its continued existence through a long period of time may explain its rapid diminution in size under adverse circumstances.

Rhinoceroses. — These animals belong to the dicerorhine phylum; that is, they are related remotely to the Sumatran, or Asiatic, and not to the African rhinoceroses, although like the latter they lack the front or cutting teeth. The stage typical of the period is the Etruscan rhinoceros (*D. etruscus*), a browsing form with short-crowned teeth, first recorded in the Val d'Arno. It appears probable that the related broad-nosed rhinoceros (*D. megarhinus* or *D. merckii*), a grazing animal with long-crowned teeth, is not certainly recognized in the Forest Bed level, but first occurs in a later interglacial stage; this point requires investigation.

Human Culture Stages

Eolithic flints. — As above noted, the earliest traces of man in beds of this age were the incised bones discovered by Desnoyers at St. Prest near Chartres in 1863. Doubt as to the artificial character of these incisions has been removed by the recent explorations of Laville and Rutot which resulted in the discovery of eolithic flints, fully confirming the discoveries of the Abbé Bourgeois in these deposits in 1867. The associated fauna includes the elephant (*E. meridionalis*), the rhinoceros (*D. etruscus*), the hippopotamus (*H. major*), the beaver (*Trogontherium*), three species of bear and one of the bison. Further confirmation is lent by the discovery of Abbott of several worked flints, two *in situ*, in the Cromer Forest Bed.

It is possible (Schötensack [1]) that the Mauer sands, containing some species of the First Fauna, as well as an elephant attributed to *E. antiquus*, are of this early date. (See pp. 401, 403).

2. The Second, or Mid-Pleistocene Fauna

Comparing the mammals of Europe now present with those demarcating the stages in the Pliocene, Miocene, and earlier ages, we perceive that we are truly entering a new life zone, which may be divided into two faunal subzones, an earlier and a more recent. (See pp. 375, 389.)

The mammals of this grand life zone have lost many resemblances to those of the Upper Pliocene and are regarded by most authorities (pp. 377, 378) as belonging chiefly to the second and third interglacial epochs. They are distinguished from those typical of the Norfolk Forest Bed by the disappearance of certain surviving Pliocene forms and by the first appearance in northern Europe of certain southern types, such as the hippopotamus and the straight-tusked elephant.

[1] Schötensack, O., Der Unterkiefer des *Homo heidelbergensis* aus den Sanden von Mauer bei Heidelberg: Ein Beitrag zur Paläontologie des Menschen. Leipzig, 1908.

The saber-tooth tigers (*Machærodus*) now disappear in Europe and their place in the balance of nature is taken by giant true leonid felines (*Felis spelæa*); the southern mammoth (*E. meridionalis*) is replaced by a more progressive stage (*E. trogontherii*), which is regarded by Pohlig as its direct successor; the polycladine deer of Upper Pliocene and Norfolk Forest Bed times have vanished, neither are there traces of the axis deer. True cattle (*Bos primigenius*) now certainly appear as well as the *Bison*. The moose (*Alces latifrons*), the giant fallow deer (*Megaceros belgrandi*), and the roe

Fig. 177. — The giant fallow deer, *Megaceros*, of the British Pleistocene, from a skeleton found in the Irish peat bogs. After original by Charles R. Knight in the American Museum of Natural History.

deer (*Capreolus*) are all present. The true stag (*Cervus elaphus*) is again recorded, but somewhat doubtfully. Another animal of somewhat doubtful record but of very great interest is the reindeer (*Rangifer tarandus*); this animal, if present, is rare, because this is distinctively the pre-reindeer period. Among other arctic forms the musk ox (*O. moschatus*) is conspicuous by its absence. As evidence of milder temperatures, the hippopotamus again appears in central Europe and in Great Britain. Rhinoceroses are very abundant, but still represent exclusively the broad-nosed types, the dicerorhine, or Sumatran phylum (*D. merckii*, or *D. megarhinus*). The brachyodont Etruscan rhinoceros (*D. etruscus*) is doubtfully recorded.

The carnivores of the period include, beside the cave lion (*Felis spelæa*), the lynx (*Felis lynx*), the brown bear (*Ursus arctos*), and the badger (*Meles*).

Among the rodents, *Trogontherium* reappears accompanied by beavers (*Castor fiber*) and marmots (*Marmota*).

It is especially noteworthy and characteristic of this fauna that it contains no types either of the cold northern steppes or of the tundras, that, beside the absence of the musk ox and the rarity of the reindeer, no arctic rodents are recorded.

The appearance of the earliest skeletal remains of man is the fact of most tremendous interest in this great life zone. Such remains are certainly intermingled with those of the mammoths and other mammals. The earliest (*Eolithic*) human stage (*Homo heidelbergensis*) belongs to the earlier phase of Mosbach, while the remains of the palæolithic (*Homo neandertalensis*) belong in the later phase of the period of Taubach and Krapina. Of these we shall speak more fully on a later page. It is important, however, to call attention again to the differences of opinion between Penck and Boule (p. 380) as to the correlation of the mammalian fauna of the geologic glacial and interglacial phases and the human culture stages.

A unit fauna. — A grandly distinctive fact is that in all the localities listed below we have a substantially similar mammalian fauna, that is, a fauna composed of similar or closely related species, which may have retreated with the advance of the ice but reappeared in interglacial times.

We note that it is the stage *prior* to the appearance of the true mammoth (*E. primigenius*), as well as prior to that of the atelodine or dicerine rhinoceroses (*D. antiquitatis*); we note the absence of the steppe and tundra types of mammals, which only arrive in a later stage, and that the fauna taken together is that of forests, river borders, and of an open meadow country, containing a mingling of hardy forms of the north, like the deer and the moose, with probably the more sensitive forms of the south.

The horse was distributed over all the northern hemisphere in the older Pleistocene, both in glacial and interglacial epochs. The specific references to *E. caballus fossilis* are very indefinite and doubtful. The horses of the long, warm, interglacial stage were remarkable for their great size, which exceeded that of the largest living breeds. According to Pohlig [1] they were at all times accompanied by wild asses (*? E. hemionus*). This, we are inclined, however, to believe was a feature of the Asiatic steppe period, in which we should expect to find asses similar to the dzegettai of Asia.

Flora of the interglacial periods. — As in the first or Norfolk interglacial, the climate was perceptibly warmer, or at least more equable and humid than at the present time. In fact, during the second long, warm interglacial and the shorter, or third interglacial period, there was a recurrence of conditions milder than the present. A vision of the flora is afforded in the Quaternary tuffs of Provence [2] which are associated with the remains of

[1] Pohlig, H., Eiszeit und Urgeschichte des Menschen. Leipzig, 1907.

[2] De Saporta, G., La Flore des Tufs Quaternaires en Provence. *C. R. Sess. Congr. Sci. France.* Aix, 1867.

the *E. antiquus* stage. "The flora of the Quaternary tuffs," observes Saporta, "is composed almost entirely of woody forms living in valleys and by the sides of streams." It is for the most part analogous with the present flora of Provence. Of the thirty-seven species, twenty-nine still occur in this region. Among the forms which have since retreated to the south are the sweet bay (*Laurus nobilis*) and another species of laurel (*L. canariensis*) which is now confined to the Canaries. The greater humidity of the time is indicated by the presence of species of pines which require more moisture. As in the Norfolk Interglacial the figs (*Ficus*) and the Judas trees (*Cercis*) flourished. The ash (*Fraxinus*) is of a species now found in Corsica and Italy. On the whole the forest trees and forest ground flora are surprisingly modern, including oaks, elms, poplars, willows, lindens, maples, sumacs, dogwood, hawthorn. Among the climbing plants are the vine (*Vitis*) and clematis (*Clematis*).

First Faunal Sub-zone

The life of this zone is typified by the fauna of Mosbach, of Rixdorf, and of Süssenborn. It is the *Elephas trogontherii* stage of Pohlig.

This stage opens with the more temperate climate of the long, warm, interglacial period known as the Mindel-Riss of Penck. This period was first observed by Lyell and Evans in England, and subsequently recognized in Germany and France. Geologically the deposits are of fluviatile origin, consisting chiefly of river sands and gravels, in which the remains of hippopotamus, of *Dicerorhinus merckii*, and of *Elephas trogontherii* occur. These animals were formerly cited as evidence of south temperate climate, but the evidence of the equally numerous northern types and the temperate flora tends to modify extreme views as to temperature.

The geographic connections of Europe with the south through the land bridges of Lower Pleistocene times still persisted, because the depression of the southern portions of the continent of Europe had not yet begun.

Among the chief localities are the following:

Mosbach, near the Neckar in northern Baden (Fig. 176, 12).
Süssenborn, near Weimar, Germany (11).
Rixdorf, near Potsdam, Germany (10).
St. Roch, France.
Clacton, Essex, England (13).
Mauer Sands, near Heidelberg (14).

The most typical fauna is that of *Mosbach*.[1] Here are found all the characteristic types of the period, the hippopotamus (*H. major*), the urus (*Bos primigenius*), the bison (*B. priscus*), the rhinoceros (*D. merckii*), two species of mammoth (*E. antiquus, E. trogontherii*), horses (*E. ? caballus*).

[1] Lepsius, R., Geologie von Deutschland und den Angrenzenden Gebieten. Erster Teil: Das Westliche und Südliche Deutschland. Stuttgart, 1892.

Among the river-living forms are the beavers; the giant beaver (*Trogontherium*) makes its last appearance in Europe in this sub-stage. The marmot (*Marmota*), now found in the Alps, Carpathians, and Pyrenees, is a mountain-living type whose remains may have been borne down by the streams. The carnivores include the lions (*F. spelæa*), lynx (*F. lynx*), the bear (*Ursus arctos*), and the badger (*Meles*). The deer family is represented by the moose, the giant deer, the roe deer, and the stag (*C. elaphus*). The former identification of the reindeer (*R. tarandus*) is now disputed. According to Lepsius the molluscan fauna points to a colder climate than the present.[1]

First Faunal Sub-Zone
Man
Homo heidelbergensis
Straight-tusked elephant
E. antiquus
Mammoth
E. trogontherii
Broad-nosed rhinoceros
D. merckii
Wild horse
Equus (?) sp.
Urus
Bos primigenius
Bison
Bison priscus
Red deer
Cervus elaphus
(?) Reindeer
Rangifer tarandus
Giant fallow deer
Cervus subgen. *Megaceros*
Moose
Alces
Hippopotamus
H. major
Giant beaver
Trogontherium
Lion
Felis spelæa
Marmot
Marmota

The gravels of *Süssenborn*[2] are of the same age as the Mosbach sands. They belong to the *Elephas trogontherii* stage of Pohlig, and this species is more abundant here than any other. The fauna again is very similar, including the broad-nosed rhinoceros (*D. merckii*), a species of horse more primitive than *E. caballus*, the bison (*B. priscus*), the red deer (*C. elaphus*), and the roe deer. Weiss also identifies here somewhat doubtfully a reindeer (*R. tarandus*).

Eolithic stage, Heidelberg Man. — To the faunal stage of *Elephas antiquus*, of the Etruscan rhinoceros (*D. etruscus*), and of primitive species of horse (*E. stenonis* [?]) is to be added the recently discovered Heidelberg man (*Homo heidelbergensis*) determined from a lower jaw found (1907)[3] in the Mauer sands at a depth of 24.10 meters. These sands are capped by deposits of loess. Schötensack likens the mammals of the Mauer sands to those of the Forest Bed of Norfolk; the presence of *E. antiquus* indicates a somewhat more recent date; while the species of horse and rhinoceros would agree with the earlier Forest Bed date. This discovery is one of the most im-

[1] Lepsius, R., Geologie von Deutschland und den Angrenzenden Gebieten. Erster Teil: Das Westliche und Südliche Deutschland. Stuttgart, 1892.

[2] Weiss, A., Die Conchylienfauna der Kiese von Süssenborn bei Weimar. *Zeitschr. Deutsch. Geol. Gesell.*, Vol. 51, 1899, pp. 156–167.

[3] Schötensack, O., Der Unterkiefer des *Homo heidelbergensis* aus den Sanden von Mauer bei Heidelberg: Ein Beitrag zur Paläontologie des Menschen. Leipzig. Verlag von Wilhelm Engelmann, 1908.

portant in the whole history of anthropology, especially as it is said to have been followed by the finding of eoliths in the same layer. The lower jaw is exceptionally massive, without chin projection, with an essentially human

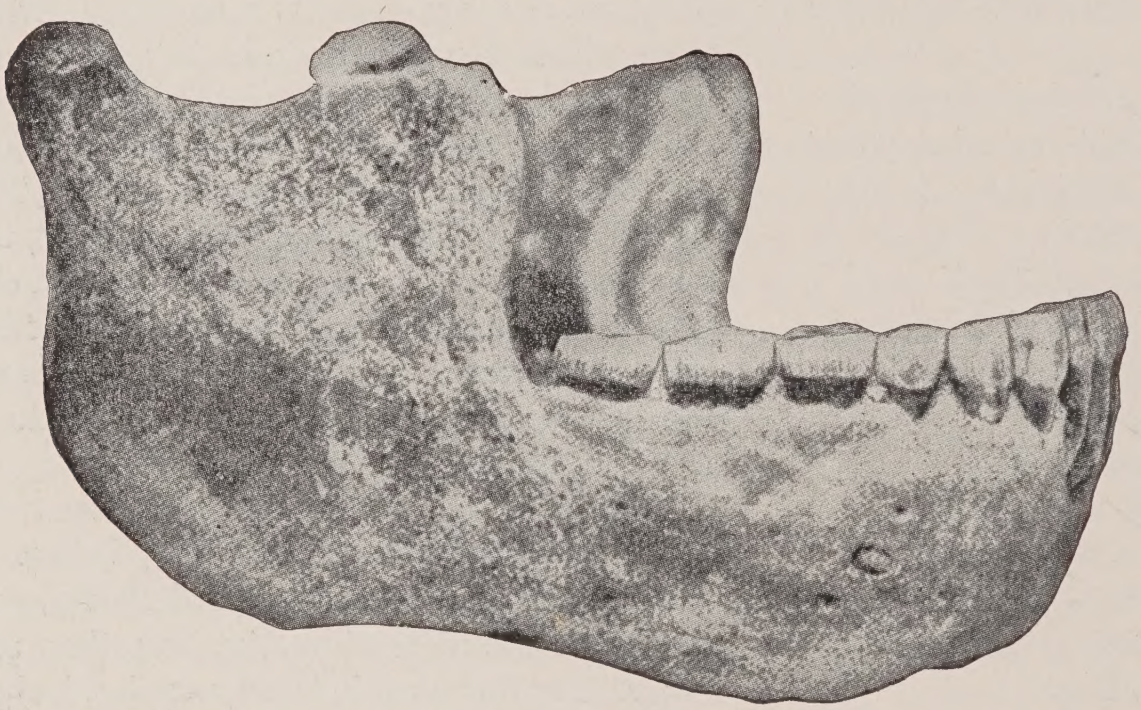


Fig. 178. — The human lower jaw (about × $\frac{3}{4}$) found near Heidelberg, on which is based the species *Homo heidelbergensis*. After Schötensack and MacCurdy.

set of teeth; in other words, it is a jaw similar to that of an anthropoid ape, with the dentition of a man. There can be little doubt that it belongs to one of the makers of the eoliths.[1]

Eolithic flints have also been found in Rixdorf as well as in Britz and Rudesdorf, near Berlin. Stations have been discovered in England and France of the same Eolithic age.

Palæolithic Stage. The Chellean. — The typical Chellean also belongs with the first life zone of the second, or mid-Pleistocene fauna. This is proven in the gravel beds of Chelles (Fig. 176, 15), situated only a few meters above the present level of the Marne, which show a succession of three distinct deposits. The earliest deposit, or the typical Chellean, at the base, resting unconformably upon the Tertiary, is a gravel containing the remains of straight-tusked elephants (*E. antiquus*), the broad-nosed rhinoceros (*D. merckii*), the giant beaver (*Trogontherium cuvieri*), together with palæolithic flint implements of human manufacture of the most primitive type. Thus the Chellean is regarded by Penck (table, p. 379) as belonging in the long, warm, Mindel-Riss interglacial epoch. Boule, however, assigns it (p. 380) a more recent age, or just preceding the last glaciation. No traces of the true mammoth (*E. primigenius*) nor of the woolly rhinoceros (*R. antiquitatis*) are found in the lower Chellean Zone; but both are found

[1] MacCurdy, G. G., Eolithic and Paleolithic Man. *Amer. Anthropol.*, Vol. II, no. 1, Jan.–Mar., 1909, pp. 92–100.

on higher levels of the same deposits, associated with flints of the *Mousterian* type, fixing the age of the higher levels as Mousterian.

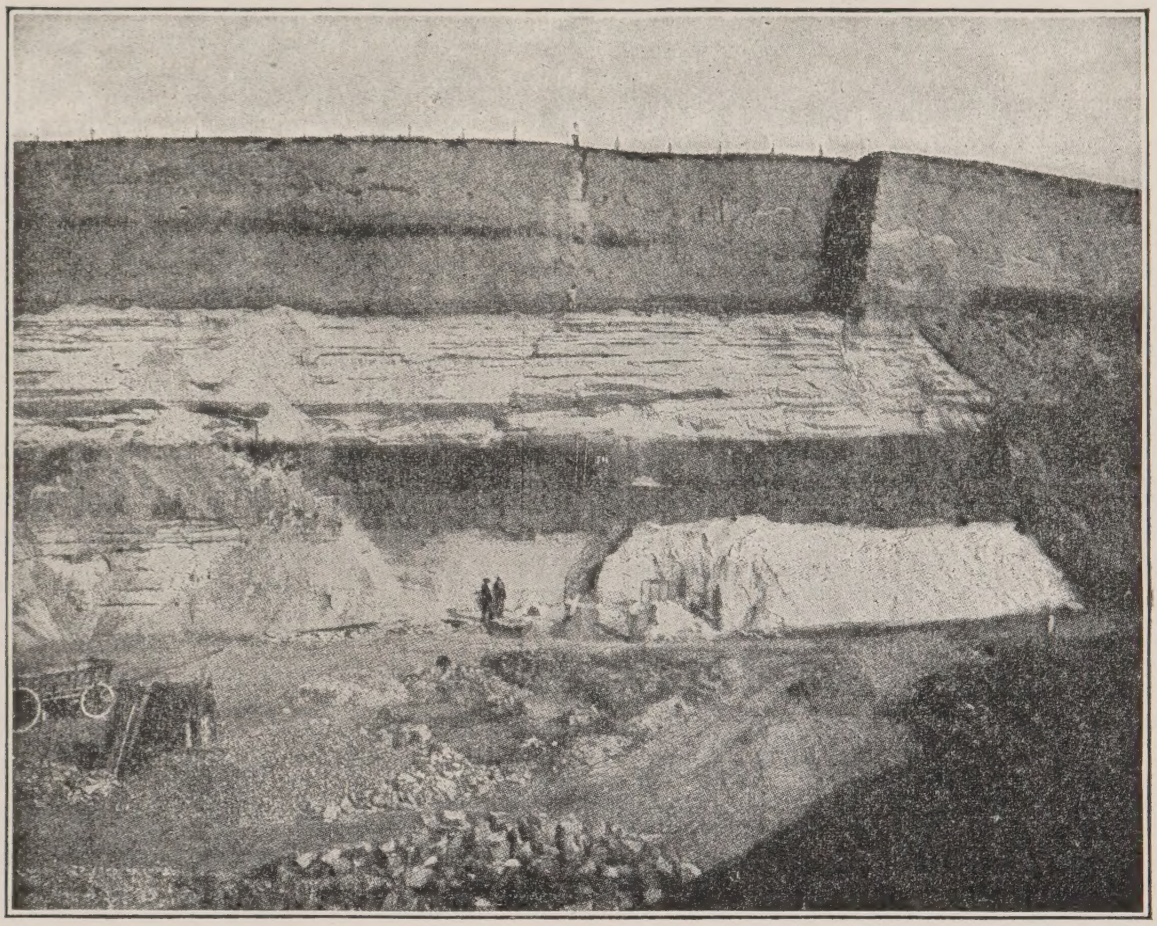


FIG. 179. — Sand-pit at Mauer near Heidelberg. The lower jaw (*Homo heidelbergensis*) was found at the spot marked with a cross. After Schötensack and MacCurdy.

Second Faunal Sub-zone

This is the *Elephas antiquus* stage of Pohlig. According to Penck it corresponds with the short, final interglacial epoch and with the Mousterian stage of palæolithic culture. It is typified by the fauna of Taubach (near Weimar) (Fig. 176, 19), the travertines of Laviste and Aygelades near Marseilles, the tuffs of the Tiber valley near Rome (21), the lignites of Utznach and Dürnten (18) near Zürich, of Grays-Thurrock and Ilford (17), Essex, England.

The straight-tusked elephant (*E. antiquus*) was very abundant, but this is its last appearance north of Italy. The most important new arrival is the true mammoth (*Elephas primigenius*), which, according to Pohlig, is a direct descendant of *E. trogontherii*, which in its turn is derived from *E. meridionalis*.[1]

The broad-nosed rhinoceros (*D. merckii*) is also abundant, but it now appears for the last time. The hippopotamus is not recorded at Mosbach, but is recorded in Essex, England (Ilford, Grays-Thurrock).

[1] Pohlig, H., Über *Elephas trogontherii* in England. *Monatsber. Deutsch. Geolog. Ges.*, Vol. LXI, 1909, no. 5.

By far the most important animal is *man*, known as *Homo neandertalensis*.

Depression. — According to Pohlig,[1] this stage is characterized geographically by the widespread depression of the continental borders of southern Europe. Great Britain was cut off from the continent, Spain from Morocco; Italy, Sardinia, and Tunis were separated, and Greece lost its connection with Asia Minor. A somewhat cooler interglacial climate is represented in the fauna of the Thuringian tufas, in which Pohlig records sixty-one species of mammals. Geologically the stage was characterized by extensive volcanic disturbances in central Europe, and by the deposition of gypsum and tufas, these earth movements being connected through the widespread depression of the continental borders and isolation of the islands of the Mediterranean above noted.

FIG. 180. — Reconstruction of the head of *Homo neandertalensis* by Charles R. Knight under the direction of the author. 1910.

The chief localities in which this fauna is recorded are the following:

GRAYS-THURROCK AND ILFORD, Essex, England (Fig. 176, 17).
DÜRNTEN, near Zürich, Switzerland (18).
UTZNACH, lignites, near Zürich (18).
TAUBACH, near Weimar, Germany (19).
LAVISTE, travertines, near Marseilles.
KRAPINA (cave of), Croatia (23 *a*).

It is interesting to summarize this fauna as found at Taubach,[2] near Weimar, also at Ilford, and Grays-Thurrock, Essex,[3] in order to bring out more clearly its contrast with that which follows:

Summary of Second Fauna

Man, *Homo neandertalensis*
Straight-tusked elephant, *E. antiquus*

This fauna is that of Taubach and of Ilford, Essex. It will be seen to present a wide contrast to the mammalian assemblage which

[1] Pohlig, H., Vorläufige Mittheilungen über das Plistocaen, insbesondere Thüringens. *Sitzungsber. Niederrhein Ges. Bonn*, Mar. 3, 1884, pp. 2–15.

[2] Pohlig, H., Vorläufige Mittheilungen über das Plistocaen, etc., 1884, p. 4.

[3] Dawkins, W. B., Classification of the Tertiary Period by Means of the Mammalia. *Quart. Jour. Geol. Soc.*, Aug., 1880, pp. 379–405.

Early mammoth, *E. trogontherii*
Broad-nosed rhinoceros, *D. merckii*
Wild horse, *E. (?) caballus*
Probably the 'forest' variety
Wild boar, *Sus (scrofa) antiquus*
Extinct variety
Bison, *B. priscus*
Extinct variety
Urus, or 'Ur-ochs,' Wild cattle
Bos primigenius
(?) Red deer, *C. elaphus*
Roe deer, *C. capreolus*
Giant deer, *C. megaceros*
(?) Reindeer, *R. tarandus*
Lion, *Felis (leo) spelæa*
Hyæna (crocuta) spelæa
Brown bear, *Ursus arctos*
Small cave bear, *Ursus spelæus*
Wolf and fox, *Canis lupus, C. vulpes*
Badger, *Meles taxus*
Marten, *Mustela martes*
Otter, *Lutra*
Beaver, *Castor fiber*
Extinct variety
Water and field vole, *Arvicola*
Hamster, *Cricetus*
Suslik, *Spermophilus*
Marmot, *Marmota*

follows in the Third Great Life Zone. At Grays-Thurrock, Essex, the hippopotamus also is recorded by Dawkins. It is noteworthy that the reindeer (*R. tarandus*) is not recorded in Essex. The mammoth of Essex was referred by Pohlig[1] to *E. trogontherii*. The horse of Essex, according to Ewart,[2] is of the 'forest' type. This fauna is a prevailing forest-meadow and river fauna. It appears probable that the lions, hyænas, and bears which occur here are not true cave types, but ancestors of the cave types which appear in the next geologic stage. They certainly were not cave-dwellers at this time, so the specific names are misleading.

Flora. — The lignites of Dürnten and Utznach reveal forests of mid-Pleistocene age, similar to those which still continue to flourish in the same region of Zürich and St. Gall, consisting of spruce, firs (*Pinus abies*), mountain pines, larches, birches, yews, and sycamores, with an undergrowth of hazel. With this hardy flora is associated the straight-tusked elephant, the broad-nosed rhinoceros, the urus, and the stag. These lignitic deposits rest on the remains of a retreating glacier, and are in turn covered with those of another glacier, and are therefore interglacial.[3]

Mammals of the Second Faunal Zone. — In considering the life it is necessary to keep in mind the 'alternate migration theory,' of the second and third faunas.

The broad-nosed rhinoceros and the straight-tusked elephant were among the most characteristic mammals of this epoch. The former animal (*D*

[1] Pohlig, H., Dentition und Kranologie des *Elephas antiquus* Falc. mit Beiträgen über *Elephas primigenius* Blum. und *Elephas meridionalis* Nesti. *Nov. Act. Ksl. Leop.-Carol. Deutsch. Akad. Naturforsch.*, Vol. LIII, no. 1, Halle, 1888, p. 326.

[2] Ewart, J. C., The Multiple Origin of Horses and Ponies. *Repr. Trans. Highl. Agric. Soc. Scotland*, 1904, p. 581.

[3] Dawkins, W. B., Early Man in Britain and his Place in the Tertiary Period. London, 1880, p. 145.

merckii) is a relative of the smaller form (*D. etruscus*) of the Norfolk interglacial, or first interglacial period, but is readily distinguished by its hypsodont or long-crowned grinding teeth. It is distinguished from all other rhinoceroses by its greater size and relatively longer legs;[1] the horn was very long, and inclined forward, the second horn seeming to have been almost equally large. The skin, so far as we know, was not clothed with hair. It left no descendants on the Mediterranean islands, nor have remains been found in Spain.

The true mammoth (*E. trogontherii*), which first occurs at this stage, is the most specialized form of elephant which has ever existed, especially in the numerous thin and closely compressed laminæ in the enamel of its teeth. Probably its most typical form is that of the northern or arctic phase of evolution (*E. primigenius*), which belongs to the third great faunal zone of the Pleistocene.

The bison (*B. priscus*) rivaled the mammoth as a wanderer, able to adapt itself to wide diversities of climate. In the long, warm, interglacial period there existed a race, *B. priscus* (*antiqui*), which enjoyed a wide distribution, while on the Mediterranean islands there lived pigmy varieties. The bison is a brachycephalic or short-headed ox, while its contemporary, the gigantic urus (*Bos primigenius*) is long-headed or dolichocephalic, also less slender and less agile than the bison. At Dürnten, remains of the urus are found associated with those of *E. antiquus* and *D. merckii*.[2] The popular Teutonic designation of these animals is rather confusing to English ears. It is:

"Auerochs," "Wisent" = *Bison priscus*.
"Ur-ochs" "Urus" (*i.e.* primitive oxen) = *Bos primigenius*.

The *urus* of Cæsar, or *Ur-ochs*, is mentioned as surviving in Germany in its wild state as late as the twelfth century A.D. The bison or *Wisent* has survived to the present time, and is now represented in the *Bos bison* or *Bison bonasus* of Lithuania, where it is carefully preserved.[2] The relations of these animals to domestication will be considered on a later page.

Horses of the Second and Third Faunal Zones. — There is bright promise of clearing up the relations of the Pleistocene horses of Europe to the modern wild and domesticated races through new lines of study instituted by Ewart[3] since 1904. The different wild breeds of horses have evolved in three great kinds of environment: thus we discover horses adapted to: (1) forests and upland valleys, (2) to high, dry steppes, (3) to deserts or plateaux. In these three chief habitats the horses may be respectively

[1] Pohlig, Eiszeit und Urgeschichte des Menschen, 1907, pp. 124–125.

[2] Pohlig, H., Eiszeit und Urgeschichte des Menschen. Leipzig, 1907, p. 131; and Rütimeyer, L., Die Fauna der Pfahlbauten der Schweiz. *Neue Denkschr. schweiz. Ges. gesam. Naturwiss.*, Vol. XIX, Zürich, 1862, pp. 68–112.

[3] Ewart, J. C., '04, '07, '09. For titles see Bibliography.

known as the 'forest horse,' the 'steppe horse,' and the 'plateau horse.' Each has its distinctive coloring, tooth structure, and proportions of skull, body, and limbs.

In the *forest* horse we see a relatively large, clumsy animal; the face is broad, short, and not bent down on the cranium, in which respect it resembles other browsing and forest-living types of Herbivora. The limbs are short, the front cannon bone (Mtc. III) being short and stout, the length only 5½ times the width. The tail is set on low. This type of horse (*E. robustus*) is found at Solutré and in the Neolithic deposits of Ilford (Essex) and in Kent.

The desert or *plateau* horse, widely differing in proportions, is the Pleistocene animal identified by Owen as an ass (*E. asinus fossilis*) but considered a horse by Ewart, and named by him *E. gracilis*. This is a small animal, not over 12.2 hands in height, slender-limbed, with long, slender front cannon bones (Mtc. III), the length being 7½ times the width. The head is small, the face fine and narrow, with a straight profile only slightly deflected upon the cranium. The internal cusp (protocone) of the upper molars is short. Remains of an animal of this type are found in the Pliocene of Italy (small, slender-limbed varieties of *E. stenonis*) and France, and in the Pleistocene of France and northern Africa. It agrees, so far as known, with the existing Celtic pony type (*E. caballus celticus*), a variety of horse distinguished by small, fine head, large eyes, slender limbs, five lumbar vertebræ, now found in more or less pure form in the outlying islands and on the coast of western Europe. This animal is believed to be a northern, hardy, thick-coated relative of the pure *desert* type, better known as the Arabian, which gave rise to the modern thoroughbred.

The *steppe* or third kind of horse is typified by the existing wild species of the Gobi Desert of central Asia (*E. przewalskii*). It is characterized by short neck, large head, with a convex profile, short back, like the Celtic pony, and only five lumbar vertebræ and heavy limbs. This type of horse is depicted in the palæolithic Magdalenian drawings of France.

Another possible contributor to the breeds of domesticated horses is an animal of the *E. sivalensis* type in the Upper Pliocene of the Siwaliks of India. This animal is tall, with long, fairly slender limbs, long neck, well set on tail, long face, strongly deflected on the cranium, with a convex profile and broad brow, and short protocone.

Life of the Mediterranean Islands. — Rütimeyer (1869) believed that Morocco, Algeria, and Tunis were stocked with animals by way of Gibraltar, and perhaps also by Sicily and Malta from Europe. In the islands of Cyprus, Malta, and Crete, as recently explored by Miss Bate,[1] we have proof first of a period of connection with the neighboring continents through elevation, second of the isolation of the islands through depression, followed

[1] Bate, Dorothea, M. A., Pleistocene Mammalia in Crete. *Geol. Mag.*, n.s., Decade 5, Vol. II, May, 1905, pp. 193–202.

by the dwarfing of several types of large mammals confined there or made captive by the sea. The occurrence of closely related but specifically different pigmy elephants and hippopotami in widely separated islands is an instance of independent evolution, with some divergence, from common ancestors. It appears probable that Cyprus became an island first. The extinct *Elephas cypriotes* and *Hippopotamus minutus* are both more primitive than the Maltese-Sicilian species. The affinity of Malta to Sicily is indicated by the common occurrence in cavern deposits on both islands of two species, *Elephas mnaidriensis* and *Hippopotamus pentlandi*. *E. melitensis*, a dwarf race characteristic of Malta, has been found also near Rome,[1] which would appear to indicate that the land connection with the Italian mainland existed probably at two different times. Pohlig believes[2] that toward the end of the first glacial period the large mammals migrated to Sicily, which at that time was connected both with Europe and Africa; the land bridges then became submerged, and the large mammals became dwarf races. The dwarf elephants (*E. melitensis*, *E. mnaidriensis*), however, are both believed to be derived from the European straight-tusked elephant (*E. antiquus*), of Asiatic origin. The African elephant (*Loxodonta*) never crossed the Mediterranean. The reduced existing fauna of Cyprus contains a mingling of European and North African forms, and shows the effects of deforestation in historic times.

Human Culture Stage

Mousterian. — The Mousterian was in part interglacial and in part glacial, corresponding, according to Penck, with the Riss, or third glacial advance, the most extensive known. We are still in the second life zone, or period of the straight-tusked elephant (*E. antiquus*) and of the broad-nosed rhinoceros (*D. merckii*), which may alternate, by migration, with mammals of the third life zone. Together with these mammals in the Prince's Cave in Monaco are found the remains of hippopotamus, but this animal does not occur to the north of the Alps at this time.

To this period belongs the fauna of the Wildkirchli Cave on Mont Sentis in Switzerland (Fig. 176, 20) and, still more important for the remains of man which they contain, the caves of Neandertal (22), in western Germany, of Spy (23) in Belgium, and of Krapina (23 *a*) in Croatia. While Penck regards this Mousterian as belonging to the third glaciation, Boule maintains that it belongs to the Würm, or fourth glaciation.[3]

This period is that of the Neandertal race of men (*Homo neandertalen-*

[1] Pohlig H., Die Cerviden des thüringischen Diluvialtravert nes mit Beiträgen über andere diluviale und über recente Hirschformen. *Paläontographica*, Vol. XXXIX, 1892, pp. 215–262.

[2] Pohlig, H., Eine Elephantenhöhle Siciliens und der erste Nachweis des Cranialdomes von *Elephas antiquus*. *Abhand. königl. bayer. Akad. Wissensch.*, München, 1893, pp. 37 seq.

[3] Boule, M., Observations sur un Silex Taillé du Jura et sur la Chronologie de M. Penck. *L'Anthropol.*, Vol. XIX, 1908.

sis),[1] the typical Palæolithic men of Europe, who were far more primitive both in skull and limb structure than the Neolithic men (see Fig. 180). The skull of Neandertal man was characterized by an extremely receding forehead, by the great prominence of the supraorbital ridges, and by a rather slender

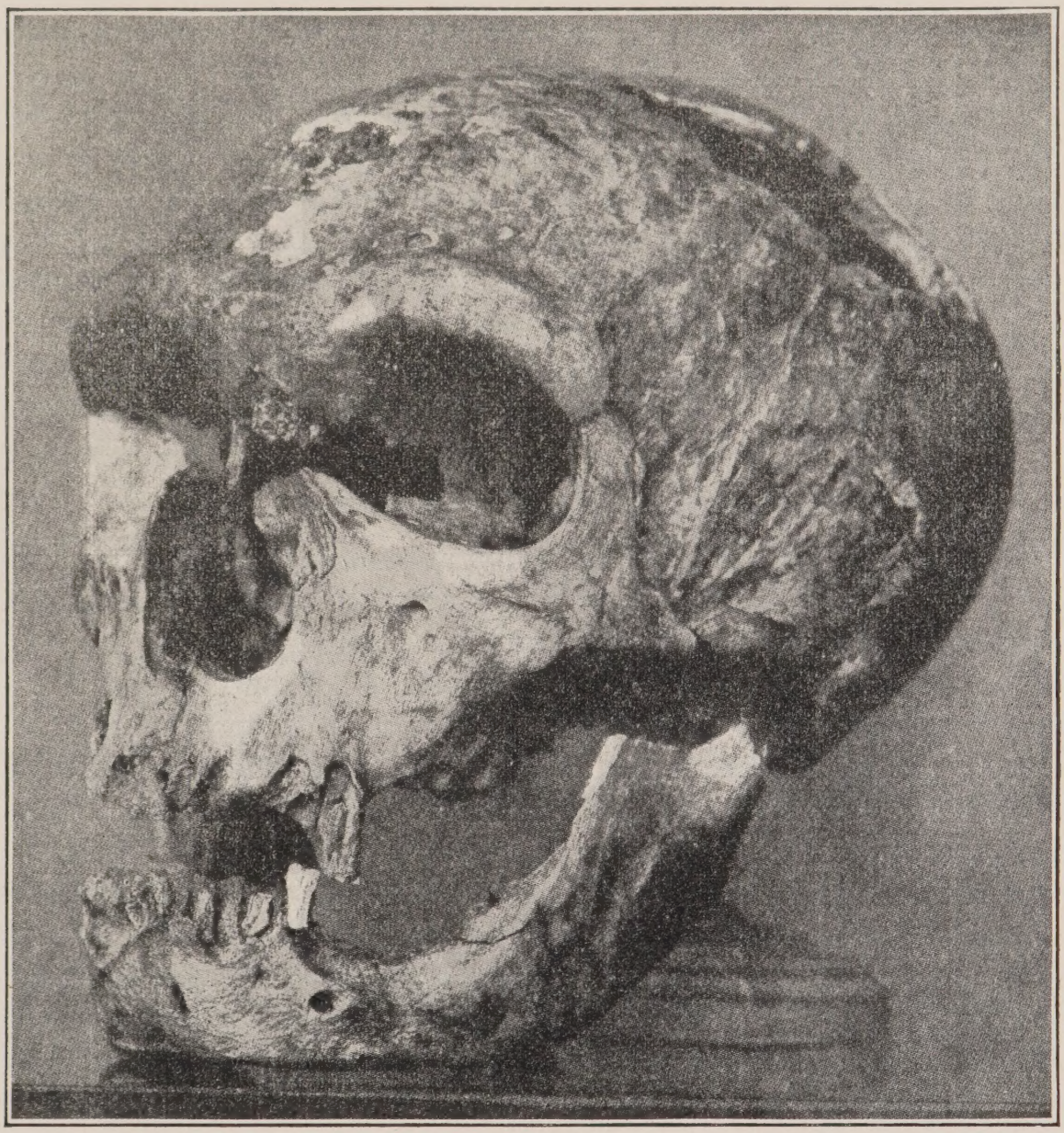


FIG. 181. — Skull of a 'Neandertal man' from the cavern of La Chapelle-aux-Saints (Corrèze), France. After Boule.

jaw. The occipital projection for the attachment of the superior muscles of the neck was large, indicating that these muscles at the back of the neck were strongly developed, a character necessary to meat-eaters before the

[1] The mid-Pleistocene man was definitely named *Homo neanderthalensis* by Cope in 1893 at the time of the discovery of the skeletons of Spy; it seems, however, that King had previously (1864) used the same term. Schwalbe (1901) remarks, . . . "the species of man which I, together with King (1864) and Cope (1893), designated as Homo neanderthalensis." In the following year (1902) the same author introduces the term *Homo primigenius*, which is that generally adopted in Germany. Among French authors the same man is known to-day as *Homo mousteriensis*. This polynomial usage serves at least to emphasize the unanimous opinion as to the distinct specific character of mid-Pleistocene man.

invention of knives and forks. This primitive type of man was shorter than the average European (that is, 5 feet 8½ inches); he is estimated of as low stature as 5 feet 3½ inches. His lower limbs were especially powerful, but his gait seems not to have been fully erect, for the knees are bent slightly forward. The human character of the classic type of Neandertal, discovered in 1857, has been confirmed by successive discoveries at *La Naulette*, *Spy*, *Krapina*, and *Malarnaud*.

The most remarkable skull of Mousterian age is that (Fig. 181) found by the Abbés J. and A. Bouyssonie and L. Bardon in the cavern of La Chapelle-aux-Saints (Corrèze) in 1908, associated with stone implements and remains of the reindeer, urus, ibex, and woolly rhinoceros. The cranium is dolichocephalic, with prominent supraorbital processes and relatively short and broad nose, weak lower jaw, lacking the prominent chin process. These characters, as well as the posterior position of the foramen magnum and the form of the palate, are distinctly simian or pro-human.[1]

3. The Third or Upper Pleistocene Fauna

This grand faunal stage is in many ways clearly defined from those which precede it; it belongs to a period of time sharply distinguished. To the anthropologist this is the close of the long Palæolithic period, including successively, or in ascending order, the Aurignacian, Solutrian, and Magdalenian cultures; to the student of past climates as represented in glacial conditions this represents the period of the last great glaciations in the Old and New Worlds, including the advance, the maximum, and the recession periods; to the geologist this is the chief time of the formation of the loess as well as of the final river gravels and sands, and glacial moraines and boulders; to the palæontologist this is the period of the reindeer (*R. tarandus*), of the giant woolly rhinoceros (*Diceros antiquitatis*) which belongs to an entirely different race from the dicerorhine type (*D. merckii*) which it replaces, and of the arctic type of hairy, or woolly mammoth (*E. primigenius*). The straight-tusked elephant (*E. antiquus*) no longer appears. The 'steppe horse' arrives in Europe; there is evidence of steppe blood in the palæolithic horse drawings of the Madeleine Cave, and in the deposits of the Rhine Valley.[2]

Still more distinctive perhaps to the zoölogist is the first certain appearance or re-occurrence in Europe of numerous small as well as large forms of the circumpolar *arctic fauna*, namely, of the *tundra fauna*, and then of the *steppe fauna*. Thus the musk ox (*O. moschatus*) returns, accompanied by large herds of reindeer, driven southward by the renewed advance of

[1] Boule, M., L'Homme Fossile de la Chapelle-aux-Saints. *L'Anthropol.*, Vol. XIX, 1909, pp. 519–525.

[2] Ewart, J. C., On Skulls of Horses from the Roman Fort at Newstead, near Melrose, with Observations on the Origin of Domestic Horses. *Trans. Roy. Soc. Edinburgh*, Vol. XLV, Pt. 3, no. 20, 1907, pp. 555–587.

the great inland ice sheet over northern and central Europe. The reindeer penetrated even into Spain and perhaps Asia Minor.[1] Similar proofs of this great and possibly repeated southerly migration of circumpolar forms are found in North America. It is well for the reader to contrast this fauna at once with that of the mid-Pleistocene above described (p. 399).

True mammoth, *Elephas primigenius*
Woolly rhinoceros, *D. antiquitatis*
Musk ox, *Ovibos moschatus*
Reindeer, *Rangifer tarandus*
Saiga antelope, *Saiga tartarica*
Asiatic wild ass, *Equus hemionus*
Arctic hare, *Lepus variabilis*
Arctic fox, *Canis lagopus*
Jerboa, *Alactaga saliens*
Ibex, *Capra ibex*
Chamois, *Rupicapra*
Wolverine, *Gulo borealis*
Cave bear, *Ursus spelæus*

This list of animals includes a large number of new arrivals, mostly from northern Europe and Asia, which partly mingled with and partly drove before them the mammals surviving from the previous period. The chief disappearances or absentees from the early fauna are the broad-nosed rhinoceros (*D. merckii*) and the straight-tusked elephant (*E. antiquus*).

The dominant and most distinctive feature of this period is, therefore, the wave, or succession of waves, of life from the extreme north; a north no longer mild and temperate, like that of Eocene, Oligocene, and Miocene times, but partly covered with snow and ice and inhabited by arctic, tundra, and steppe types, as it is to-day.

The chief localities where this grand third fauna has been discovered are the following:

Localities	*Culture Zones*
Kesslerloch Cave, near Thayngen (Fig. 176, 37)	Magdalenian Stage
Schweizersbild Cave, near Schaffhausen (37)	Magdalenian Stage
Scattered deposits in Thuringia, in northern Germany, Saalfeld, Gera, Jena, Leipzig (29, 30, 31)	Aurignacian and Solutrian Stages
Würzburg, Bavaria, Loess deposits (33)	
Swabia and Franconia, cave deposits	Solutrian
Vöklinshofen, Alsace (28)	Aurignacian and Solutrian Stages
Montmaurin Cave (Haute-Garonne), Upper levels (35)	Magdalenian Stage
Châteauneuf-sur-Charente (Charente) (36)	

To understand the mammals of the third and fourth periods of Pleistocene life in Europe it is, first of all, necessary to group them into four great series which broadly correspond with the great geographical life zones of

[1] Pohlig, H., Dentition und Kranologie des *Elephas antiquus* Falc. . . . *Nov. Act. Ksl. Leop.-Carol. Deutsch. Akad. Naturforsch.*, Vol. LIII, no. 1, Halle, 1888.

the northern hemisphere at the present time. Here we may refer to the masterly researches of Nehring[1] and Woldrich.[2]

Pleistocene and Recent Habitat Zones

I. Tundra, or Snow-loving Fauna

Musk ox, *Ovibos moschatus*
Reindeer, *R. tarandus*
Arctic hare, *Lepus variabilis*
Banded lemming, *Myodes torquatus*
Wolverine, *Gulo borealis*
Marmot, *Arctomys bobac*
Vole, *Arvicola nivalis*
Ermine, *Fœtorius erminea*
Arctic fox, *Canis lagopus*

Ptarmigan, *Lagopus alpinus*

II. Steppe Fauna, on High, Grassy Steppes, and Pastures

Saiga antelope, *Antilope saiga*
Reindeer, *R. tarandus*
(Barren ground variety)
Wild ass, *Equus hemionus*
Wild horse, *Equus przewalskii*
(Steppe type)
Wild cattle, *Bos primigenius*
Jerboa, *Alactaga jaculus*
Suslik, *Spermophilus*
Hamster, *Cricetus*
Woolly rhinoceros, *Diceros tichorhinus*
Elasmothere, frontal-horned rhinoceros, *Elasmotherium*
Marmot, *Marmota*
Dwarf pica, *Lagomys pusillus*
Vole, *Arvicola*
Wolf, *Canis lupus*
Rabbit, *Lepus timidus*
Mole, *Talpa europœa*

III. Forest Fauna, Chiefly Forest-loving Forms

Reindeer, *R. tarandus*
(Woodland variety)
Moose, *Alces palmatus*
Red deer, *Cervus elaphus*
Roe deer, *Cervus capreolus*
Wild cattle, *Bos primigenius*
Wild boar, *Sus scrofa*
Beaver, *Castor fiber*
Vole, *Arvicola glareolus*
Dormouse, *Myoxus*
Forest mouse, *Mus sylvaticus*
Wolf, *Canis lupus*
Forest horse, *E. caballus* (Forest type)
Fox, *Canis vulpes*
Brown bear, *Ursus arctos*
Wolverine, *Gulo luscus*
Pine marten, *Mustela martes*
Badger, *Meles taxus*
Wild cat, *Felis catus*

Forest grouse, *Tetrao europalis*

IV. Forest and Field Types

Wild cattle, *Bos primigenius*
Bison, *Bison priscus*
Reindeer, *Rangifer tarandus*
Giant deer, *Cervus megaceros*
Wild horse, *Equus caballus*
Woolly rhinoceros, *D. antiquitatis*
Woolly elephant, *Elephas primigenius*

[1] Nehring, A., Über Tundren und Steppen der Jetzt- und Vorzeit, mit besonderer Berücksichtigung ihrer Fauna. Berlin, 1890.

[2] Woldrich, J. N., Die diluvialen Faunen Mitteleuropas und eine heutige Sareptaner Steppenfauna in Niederösterreich. *Mitth. Anthrop. Ges. Wien*, Vol. XI, n.s., Vol. I, Vienna, 1882.

As indicated in the repetition in the above columns, the mammals are not all closely confined to these life zones; but certain of them, especially the elephants, bison, reindeer, the rhinoceroses, and probably the primitive cattle and arctic hare, wandered freely and had a wide range. Other forms, like the musk ox, jerboa, the saiga antelope, the moose, are each respectively distinctive of the tundra, steppe, or forest environment.

Tundra fauna and flora. — Animals like the lemming [1] (*Myodes torquatus*), adapted to extreme conditions, generally cling to these very obstinately, and perish rather than conform to altered environment. This animal dwells immediately to the north of the region of coniferous forests, among scattered shrubs of the common juniper (*Juniperus communis*) and the dwarf birch (*Betula nana*). Thus we may be perfectly certain that the lemmings discovered in England, France, Belgium, and a large part of Germany in Pleistocene times are proofs of conditions which prevailed, similar to those of the present circumpolar region. The lemmings probably advanced south with the characteristic tundra fauna, and we must conclude that there were tundras in central and western Europe for a time during the Pleistocene. At Thiede near Braunschweig, the classical locality for lemming, the remains are associated solely with those of the arctic fox, arctic hare, reindeer, musk ox, and mammoth; thus a comparison of northern Eurasia and the 'barren grounds' of northern Asia and North America is quite justifiable. Characteristic plants of the period are the dwarf birch (*Betula nana*), polar willow (*Salix polaris*), mountain dryas (*Dryas octopetala*). The lemmings probably dwelt in the immediate neighborhood of the glaciers. As the climate grew warmer they retreated with the tundra fauna to the north, the high grassy slopes of the mountain sides being the last to be deserted. The arctic hare (*Lepus variabilis*) in the British Isles is now confined to Ireland and the mountains of Scotland.

As the lemming is typical of the tundras, the jerboa (*Alactaga*) is typical of steppe conditions; thus the succession of three rodents indicates approximately the succession of tundra, steppe, and forest conditions, as follows:

Tundra, the lemming (*Myodes torquatus*)
Steppe, the jerboa (*Alactaga jaculus*)
Forest, the squirrel (*Sciurus vulgaris*)

Steppe fauna. — This fauna in deposits at several different points is definitely proved to have followed the tundra fauna. Both Nehring [2] and Woldrich [3] hold that the steppes of central Europe were post-glacial. According to Woldrich (1896) the tundra and steppe types of Europe represent the

[1] Nehring, A., Über Tundren und Steppen der Jetzt- und Vorzeit, mit besonderer Berücksichtigung ihrer Fauna. Berlin, 1890, pp. 81–166.

[2] Nehring, *op. cit.*, 1890, p. 222.

[3] Woldrich, J. N., Ueber die Gliederung der anthropologischen Formationsgruppe Mitteleuropas. *Sitzber. kgl. böhm. Ges., math. naturwiss. Classe*, 1896. *Ref. Matiegka in Centralblatt Anthrop.*, 1896, pp. 142–143.

last great glacial advance, after which came the meadow or field (*Weide-fauna*), and then the forest fauna (*Wald-fauna*).

Steppe conditions of climate were rendered possible in Europe by the elevation and extension of the land much farther to the north and north-

Fig. 182. — Map of northwestern Europe in the late Pleistocene. Former coast represented at present 100 fathom line by double lines. Dots indicate areas where remains of late Pleistocene, terrestrial mammals have been found. After Boyd Dawkins.

west than at present; Great Britain was united with the continent, Scandinavia with Spitzbergen, and thus all tempering influences of the Atlantic ocean were cut off from northern Europe. Prevailing east winds probably helped to give central Europe a cold, dry continental climate favorable to dust storms. This was a chief period of loess formation, which, according to

the theory of Richthofen, owes its origin to wind-borne dust and sand acting under the influence of a dry, steppe climate both in summer and winter. However, Kobelt[1] and Scharff[2] (1899, p. 212) agree in thinking that the presence of steppe mammals affords no proof of the steppe character of the country.

The steppe regions of northern Asia still maintain this fauna. Such animals as the jerboa, which are unable to swim, presumably crossed the rivers while these were frozen over. The absence of fossil plants in the deposits of the steppe period is due to the unfavorable conditions for the preservation of plant remains. Small stretches of woodland were probably confined to the banks of rivers, to favorable mountain slopes, etc. The flora was probably like that of eastern Eurasia or southwestern Siberia to-day.

The fauna included, beside the jerboa, the rufous sizel, or suslik (*Spermophilus rufescens*), the bobac marmot (*Marmota bobac*), the dwarf pica, the hamsters, the northern voles, the corsac fox (*Canis corsac*), the manul, or Pallas's cat (*Felis manul*). Covering the plains were the larger grazing animals such as the saiga antelope, the wild asses (dzeggetai), and the wild horses, probably similar to the still surviving *Equus przewalskii*. Ewart considers it probable that the Celtic pony (*E. caballus celticus*) also came with the steppe fauna, while the yellow dun, "Norse" horse, or forest type, belongs to the succeeding forest fauna. There is evidence of 'steppe blood' in the horses of the Pleistocene deposits of the Rhine valley and in the horses of the Palæolithic drawings of the Magdalenian caves, while there is evidence of 'Celtic blood' in the horses of the mammoth beds of Britain.

The saiga antelope has now retreated to the steppes of eastern Europe and western Siberia. The jerboa (*Alactaga jaculus*) is now confined to Eurasia and western Siberia. The bobac marmot (*Marmota bobac*) has a similar range.

The characteristic fauna of the modern Alps is mainly of central Asiatic rather than of Siberian origin.[3]

Forest fauna. — Following the retreat of the glacial cap and the gradual depression of northern Europe came a more humid climate, favorable for reforestation. Besides the common squirrel (*Sciurus vulgaris*), the herald of forest conditions all over the northern hemisphere, there appeared the red deer, the roe deer, the moose, the wild boar, the red fox, the badger, the wolverine, the pine marten, the pole cat (*Fœtorius putorius*), the ermine, and the common weasel (*Mustela vulgaris*).[4]

With these still living species were mingled the great extinct mammals of the times, and occasionally these three great faunas are found pure, or

[1] Kobelt, W., Die Verbreitung der Tierwelt. Gemässigte Zone. Leipzig, 1902.
[2] Scharff, R. F., The History of the European Fauna. London, 1899.
[3] Scharff, R., The History of the European Fauna. London, 1899 (p. 340).
[4] Kobelt, W., Die Verbreitung der Tierwelt. Gemässigte Zone. Leipzig, 1902.

entirely distinct and separate, as in the lower deposits of Thiede near Braunschweig, above cited. More often they are successive, or superposed upon each other, even in the same localities; thus in the loess near Würzburg, Bavaria, Nehring [1] has recorded both a tundra and a steppe fauna, including, beside the still living types, the woolly rhinoceros, the mammoth, the urus, and the bison. In other localities Nehring has observed and most accurately recorded a vertical succession of tundra, steppe, and forest mammals.

Our realization of the long periods of time in which these successive deposits with successive faunas accumulated is intensified by their association with successive stages in the evolution of human culture. The most famous instance of this kind is that recorded by Nehring [2] in the remarkable grotto at Schweizersbild near Schaffhausen, in which the following layers appear:

Neolithic	5. Gray culture layer, forest fauna
Palæolithic	4. Upper Breccia, or 'upper rodent' layer, steppe fauna
Palæolithic	3. Yellow culture layer, palæolithic 'reindeer age,' steppe fauna
Palæolithic	2. Lower Breccia, or 'lower rodent' layer, animal remains and traces of man, tundra fauna
Palæolithic	1. Diluvial layer. No fossils

Of these the 'lower rodent' layer (2) contains a pure arctic fauna, such as the vole, hare, fox, the reindeer, the ptarmigan. In the layer above these the early steppe animals begin to appear, the hamsters and picas. Then in the 'yellow culture' layer there is an assemblage of pure steppe forms, susliks, dwarf picas, and wild horses, all pointing to the absence of forests; but at the top of this layer the first squirrel appears as the harbinger of forests. In the upper rodent (4) layer the steppe fauna begins to be intermingled with an increasing number of forest types, such as squirrels, dormice, and the pine marten. Finally we reach the (5) 'gray culture' layer, composed of the modern forest dwellers, such as the squirrel, the beaver, the pine marten, the stag, the roe, the wild boar, the brown bear. A similar succession of tundra, steppe, and forest faunas has been observed in many parts of central Europe.[3]

Elaphine or red deer.[4] — Sir Victor Brooke held that the Cervidæ originated in Asia and from there spread east and west. The Asiatic origin of the red deer has since been ably maintained by Köppen. A very large antlered race has been discovered and identified by Nehring as *C. canadensis.*

[1] Nehring, A., Übersicht über vierundzwanzig mitteleuropäische Quartär-Faunen. *Zeitschr. Deutsch. Geol. Ges.*, 1880, pp. 468–509.

[2] Nehring, A., Die kleineren Wirbeltiere vom Schweizersbild bei Schaffhausen. *Neue Denkschr. allg. schweiz. Ges. gesam. Naturwiss.*, Vol. XXV, 1896, pp. 40–77.

[3] Nehring, A., Die kleineren Wirbeltiere vom Schweizersbild bei Schaffhausen. *Neue Denkschr. allg. schweiz. Gesell. gesam. Naturwiss.*, Vol. XXXV, 1896, pp. 40–77.

[4] Scharff, R. F., The History of the European Fauna. London, 1899, pp. 246–251.

The giant fallow deer is found in Ireland, England, Scotland, the Isle of Man, France, Denmark, Germany, Austria, northern Italy, and Eurasia, even in Siberia.

Migration. — The crowding out of the tundra fauna occurred in the following manner.[1] The great alpine glaciers still extended far out over the land during the formation of the *lower rodent layer*. As these retreated they left desolate stretches behind them and the valleys and plateaux now free from ice became tundras, where swamps alternated with patches of polar willows and stunted fir trees and places covered merely with low scrubby birches or reindeer moss and lichens. As this vegetation retreated north and south before the advance of the steppe climate, the tundra fauna followed, the forms that moved south being confined to ever smaller areas and higher altitudes. Enormous intervals of time elapsed between the deposition of the (3) yellow culture layer of the reindeer age and the (5) gray culture layer of Neolithic times and the forest fauna. It was a slow change that drove the steppe mammals gradually toward the dry regions of the east to make room for the forests and their faunas. It is clear that the north and the east were the only directions open to them in their retreat before the increasingly damp climate and the spread of woodlands. The typical central European forest forms, the wild cat, marten, bear, hare, roe, stag, and urus, which constituted the principal fauna of the succeeding stage and of all later, prehistoric, and early historic time, was probably in existence long before, but confined to small and scattered bits of forests on mountain slopes and in gullies. The interval between these yellow and gray culture layers in human history means the change from the Palæolithic reindeer stage to the Neolithic stage, because in the 'gray culture' layer we find weapons and implements of polished stone which represent a stage of culture similar to that of the Swiss lake dwellings.

Mammals of the Third Faunal Zone

Mammoths. — The mammoth (*E. primigenius*) now reaches the height of its evolution and specialization. As preserved in the frozen tundras of northern Siberia it is the most completely known of all fossil Mammalia, with its undercoat of wool and overcoat of long hair. As recently described by Salensky [2] from the wonderfully complete specimen discovered in 1901 on the banks of the Beresowka River in northeastern Siberia, this animal developed characters which absolutely exclude the possibility of its ancestry to the existing Indian elephants. The hind foot is four-toed, or tetradactyl, and not five-toed as in the living forms. The head

[1] Studer, T., Die Tierreste aus den pleistocænen Ablagerungen des Schweizersbildes bei Schaffhausen. *Neue Denkschr. allg. schweiz. Ges. gesam. Naturwiss.*, Vol. XXXV, 1896, pp. 1–38.

[2] Salensky, W., Über die Hauptresultate der Erforschung des im Jahre 1901 am Ufer der Beresowka entdeckten männlichen Mammutcadavers. *C.R. Séa. Six. Congr. Internat. Zoöl. Berne*, 1904, pp. 67–86.

was larger as compared with the length of the body than in recent elephants, a character which stands in close connection with the enormous development of the tusks; these were distinguished by their spiral form, the points directed inward. The ears were very small and covered with hair. The tail was relatively shorter than in the existing elephants and was provided with a tassel of long, bristly hair at the end. The color of the hair is a yellowish brown, varying from light brown to pure brown, and a coat of woolly hair, 2 to $2\frac{1}{2}$ cm. in length, covered the whole body.

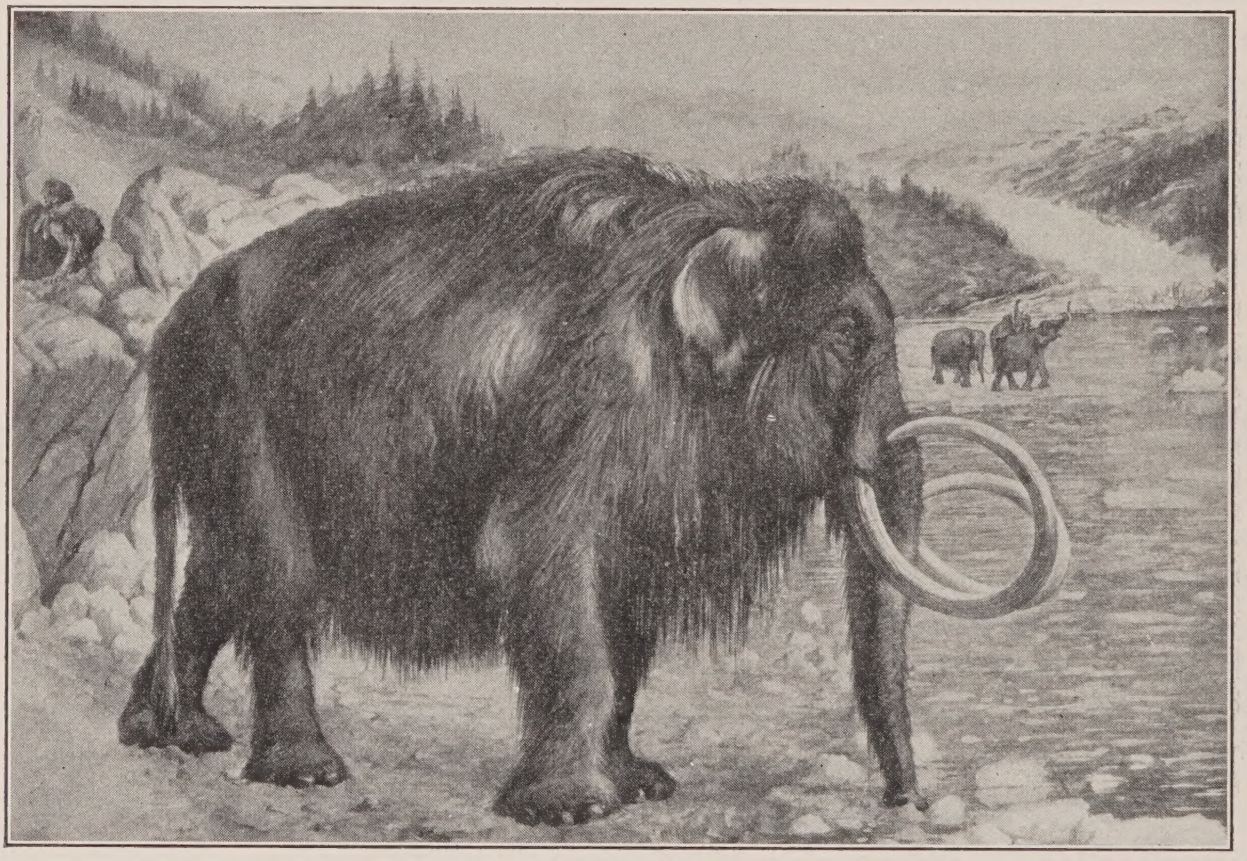


FIG. 183. — The hairy mammoth (*Elephas primigenius*) and Palæolithic man (*Homo neanderta-lensis*). After original by Charles R. Knight in the American Museum of Natural History.

Interspersed with these were a large number of longer and thicker hairs which formed mane-like patches on the cheeks, on the chin, on the shoulders, flanks, abdomen, etc. A broad fringe of this long hair extended along the sides of the body as depicted in the palæolithic sketches from the Combarelles Cave discovered by Capitan and Breuil in 1901. Especially interesting is the food found in the stomach and mouth, which consists of a meadow flora such as characterizes this region of Siberia at the present day, thus appearing to disprove the theory that the climate was milder than that now prevailing. Nor does it appear that it was more frigid, because there are few representatives of tundra vegetation. Grasses (*Gramineæ*) and sedges (*Cyperaceæ*) predominate. There were also wild thyme (*Thymus*), beans of the wild oxytropis (*Oxytropis campestris*), seeds of the alpine poppy (*Papaver*), and the boreal variety of the upright crowfoot (*Ranunculus acer*), all still found in this region.

Rhinoceroses. — It is important to recall the fact (p. 412) that the companion of the mammoth, the tichorhine or woolly rhinoceros (*D. antiquitatis*) is not a successor of the dicerorhine series (*D. etruscus, D. merckii*), but a relative of the African type of rhinoceros,[1] which had no representatives in Europe after Miocene times. It will be recalled that in the Upper Miocene (p. 264) we found in the *D. pachygnathus* of Pikermi a relative of the existing white and black rhinoceroses (*D. simus, D. bicornis*) of Africa. A remarkably preserved specimen of *D. antiquitatis* in the St. Petersburg Museum

FIG. 184. — The woolly rhinoceros (*R. antiquitatis*). The skull in this drawing is probably represented somewhat too short and the anterior horn less long and slender than it should be. The body and limbs are also too slender. After original by Charles R. Knight in the American Museum of Natural History.

shows the side of the face still covered with golden brown wool; other parts of the body were provided with a thick hairy covering. These animals were extremely long-skulled, like the white rhinoceros (*D. simus*) of Africa. They exceeded in size the existing African species, and like them bore extremely slender anterior horns, over a yard in length.[2] All the horns of this variety that have been found are more or less worn on the outer side of the bend; there was a second very short horn behind the large one. The woolly rhinoceros was more closely confined to the edge of the great ice sheet than the mammoth; that is, it did not migrate so far to the south, stopping at the Alps, while the mammoth wandered into Italy as far south as Rome.

The elasmothere (*Elasmotherium*) was another companion of the mam-

[1] *I.e.* the white rhinoceros, *Diceros simus.*

[2] Pohlig, H., Eiszeit und Urgeschichte des Menschen. Leipzig, 1907, p. 122.

moth, distributed in eastern Europe, Germany, and southern Siberia. Whether it reached northern Siberia with the mammoth, woolly rhinoceros, musk ox, and reindeer remains an open question. To the south, teeth have been attributed to this animal from Sicily.[1] It is a gigantic animal distinguished from all the European Pleistocene forms by the absence of the anterior horn and possession of an enormous horn situated on the forehead between the eyes, and by the elaborate foldings in the enamel of its teeth. It is possibly descended[2] from the typical *Aceratherium* of the Upper Miocene of Eppelsheim (p. 272), which shows the rudiment of a horn between the eyes. The skull attains a meter in length; the dermal horn on the forehead was enormous. The limb bones exceeded in size those of the largest species of rhinoceros by one-third in length. Its hypsodont and folded teeth were especially adapted to a grassy diet, and Gaudry connects its appearance in Europe with the extensive deforestation accompanying the steppe and tundra periods of mammalian life; it apparently wandered into Europe from central Asia and never became very numerous.

Reindeer or caribou. — The reindeer of Eurasia and America embrace two groups of species, the 'barren ground' and the 'woodland,' readily distinguished by the size and the proportions of the antlers.[3] The barren ground reindeer is said to have entered Europe with the second fauna and perhaps came by a different route (*i.e.* via Greenland).[4] The woodland first appears in Europe with the third fauna, and persisted until comparatively recent times, but has now become extinct. In the barren ground, typified by the Old World reindeer (*R. tarandus, R. spitzbergensis*), and by the American arctic forms (*R. arcticus, R. grœnlandicus, R. granti, R. pearyi*), the antlers are round, slender, and long, in proportion to the relatively small size of the animal, while the beam and the tines, including the brow tine, are, as a rule, but little palmated; in some forms the 'brow tine' is palmate. The antlers of the woodland group, now extinct in Europe, but typified by several American species (*R. caribou, R. montanus, R. osborni*), are heavier, flatter, thicker, and more heavily palmated, both on the beam and tines, especially the brow antler, while the tine above the 'brow,' corresponding to the 'bez-tine' of the stag (*Cervus*) is elaborately developed and palmated, contrasting sharply with the same tine in the barren ground group.

Carnivores. — Probably the chief enemies of the Herbivora were the

[1] Brandt, J. F., Mittheilungen über die Gattung *Elasmotherium*, besonders den Schädelbau derselben. *Mém. Acad. Impér. Sci. Pétersbourg*, Ser. VII, Vol. XXVI, no. 6, St. Petersburg, 1878; and Gaudry and Boule, Matériaux pour l'Histoire des Temps Quaternaires. 3ième Fasc. L'Elasmotherium. Paris, 1888.

[2] Osborn, H. F., Frontal Horn on *Aceratherium incisivum*. Relation of the Type to *Elasmotherium*. *Science*, n.s., Vol. IX, no. 214, Feb., 1899, pp. 161–162.

[3] Grant, Madison, The Caribou. *Ann. Rept. N.Y. Zoöl. Soc.*, no. 7, New York, 1892, pp. 175–196.

[4] Scharff, R. F., The History of the European Fauna, London, 1899, p. 154.

Upper Pleistocene lions (*Felis spelæa*), descended from the great cats of the Pliocene of France and Italy (*Felis arvernensis*). The fact that the remains of this animal are so often found together with those of the cold fauna makes Nehring's suggestion [1] seem plausible that the cave lion was a northern race of the recent African and West Asiatic lion, adapted to a colder climate and with heavy fur. These lions are known from deposits in England, Belgium, Austria, southern Russia, France, Spain, and Italy, Sicily, Greece, and Algeria.[2] After examination of available specimens from central and northern Europe, Boule[2] reaches the conclusion that they are not remains of tigers as was formerly supposed by de Blainville and Lartet. While rich in individual variations, *F. spelæa* is nearer the lion than the tiger in some of its characters; it should, in fact, be considered a veritable race of the recent lion with the name *Felis leo spelæa*. It sometimes equals and often surpasses the existing lions and tigers in size. It differs from both in the more gentle and uniform slope of its profile, and in its large, flat forehead, but its limb bones are longer and proportionately thicker.

The bears (*Ursus spelæus*) were far more numerous than the lions, including a gigantic and a smaller variety (*Ursus sub-spelæus*). The former nearly equaled the largest recent bears in size, and all of the cave bears were more thickset than any of the recent species. The front paws were of tremendous size. When one considers that the claw-bearing phalanges are feebly developed, that the anterior premolars are practically lost, and that the cusps of the teeth are blunted in a way which is indicative of an omnivorous diet, it becomes plain that the large Herbivora and even primitive man found no very formidable enemy in the cave bear. While the large and small races of *U. spelæa* were contemporary, there are certain indications that the smaller was the older, being found at Mosbach during early interglacial deposits. Both races became extinct in the Pleistocene without leaving descendants. The ancestor of the brown bear (*Ursus arctos priscus*), believed to be a descendant of the Etruscan bear of the Norfolk interglacial, is also found in Pleistocene caves; it is not so large as the cave bear, but while it has been mistakenly identified with the grizzly (*Ursus horribilis*), in reality it has closer affinities to the European brown bear (*Ursus arctos*).

The cave hyæna (*Hyæna crocuta spelæa*) and the cave wolf (*Canis lupus*) of the same period also attained dimensions greater than their living allies.[3] The cave hyæna is merely a variety of the living spotted hyæna (*Hyæna crocuta*) of east Africa. It has the larger proportions, the heavier build, the broad skull, the long, powerful carnassial teeth that distinguish the

[1] Nehring, A., Über Tundren und Steppen der Jetzt- und Vorzeit, mit besonderer Berücksichtigung ihrer Fauna. Berlin, 1890.

[2] Boule, M., Les Grands Chats des Cavernes. *Ann. Paléont.*, Vol. I, Paris, Jan., 1906, pp. 20–27.

[3] Gaudry, A., and Boule, M., Matériaux pour l'Histoire des Temps Quaternaires. 4ième Fasc. Les Oubliettes de Gargas. Paris, 1892, pp. 108–112.

spotted hyæna from the striped hyæna (*H. striata*) of the present day. Although proportionately heavier, the hind limbs may have been shorter than in the spotted hyæna, perhaps an adaptation to cave life which the inclement climate made necessary. Thus the Pleistocene species of European hyænas underwent an evolution of their own, and as a result the living African forms differ more from the Pleistocene hyænas than they do from those of the Pliocene. In the caves of southern France a variety (*Hyæna prisca*) of the striped hyæna (*Hyæna striata*) also occurs, where are discovered further remains (*H. intermedia*) resembling the cave hyæna. The cave hyæna was a very common animal, and is responsible for the destruction of vast numbers of the bones of its contemporaries in a manner not pleasing to the palæontologist. According to the same authorities [1] (p. 117 seq.) no constant osteological differences can be determined between the Pleistocene cave wolf and the wolf of western Europe, although the former is of considerably larger size.

The badger (*Meles taxus*) probably originated in west central Asia; the only three other species known are confined to Asia. The two extinct Lower Pliocene species are found in Persia, Maragha (*M. polaki*, *M. maraghanus*).[2]

Herbivores. — The large ruminant Herbivora of this period, the bison, the urus, and reindeer, were widely distributed but not contemporaneous, since they are chiefly characteristic of different life zones. The most typical ruminant of the tundras, the musk ox (*O. moschatus*), sometimes occurs, but is by no means common.

Especially interesting is the appearance of the alpine ruminants, the chamois (*Rupicapra tragus*), and the ibex (*Capra ibex*).

Woldrich [3] has pointed out that the large herbivores were more closely bound to their special conditions of environment, and thus more closely reflect the changes of environment, than the carnivores, which continue from one fauna into the next. Thus the bear, the lion, and the hyæna continue from one period into the next. The horse showed itself adaptive because it continued through steppe times into the meadow and into the forest period; it is probable that this was not a case of transformation but of migration of types especially fitted to these habitats, namely, of 'steppe' and 'forest' horses. No 'tundra' horse is known, although remains of horses occur in frozen tundras even bordering the Arctic Ocean (see Alaska, p. 470). The reindeer also continued in the forests of Germany after the time of Cæsar, and in the forests of Scotland probably as late as the twelfth century.

[1] Gaudry, A., and Boule, M., Matériaux pour l'Histoire des Temps Quaternaires. 4. ième Fasc. Les Oubliettes de Gargas. Paris, 1892, pp. 108–112.

[2] Scharff, *op. cit.*, 1899, p. 44.

[3] Woldrich, J. N., Die diluvialen Faunen Mitteleuropas und eine heutige Sareptaner Steppenfauna in Niederösterreich. *Mitth. anthrop. Ges. Wien*, Vol. XI, n.s., Vol. I. Vienna, 1882.

Geographic Distribution of the Third Fauna

The *Schweizersbild Cave* (Fig. 176, 37) belongs to the Magdalenian Stage of human culture, and according to Penck the indications are that it dates from the maximum period in the last glacial advance.[1] The deposits in the Schweizersbild Cave, as described above (p. 418), began with the tundra fauna, on which accumulated (1) the steppe fauna of the reindeer age, (2) the steppe fauna of the upper rodent layer, both Palæolithic, and immediately succeeded (3) by the Neolithic 'forest fauna' of the 'gray culture' layer. It thus bridges over an enormously long period of time.

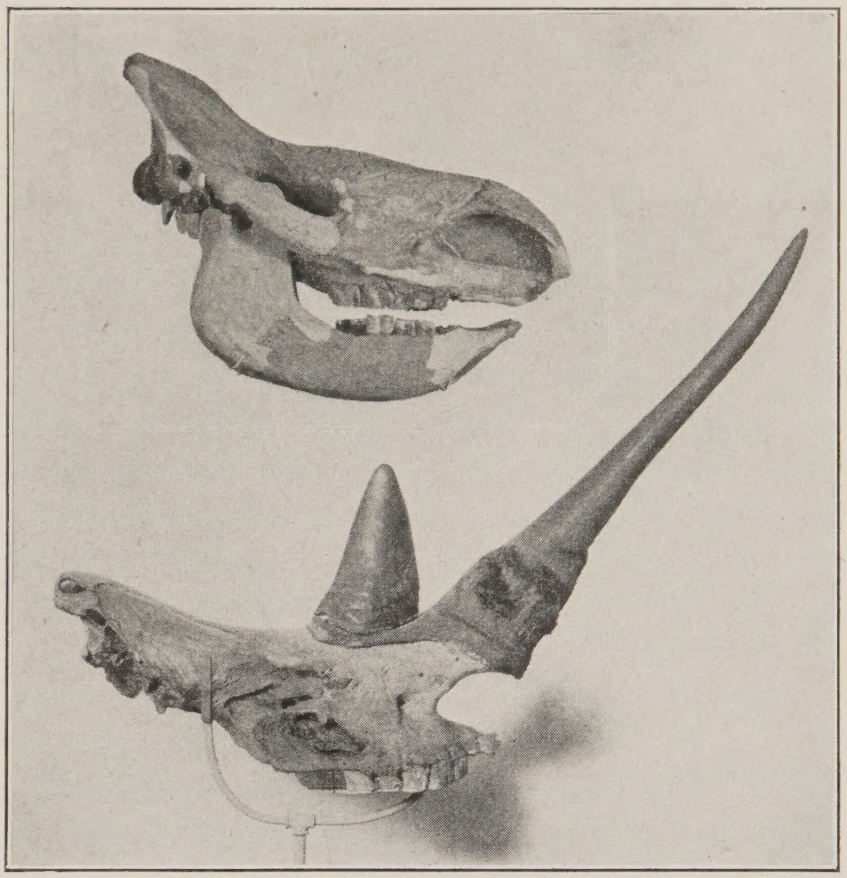


FIG. 185. — Skulls of the Pleistocene "woolly rhinoceros" *D. antiquitatis* of Eurasia (above), and of the recent African "white rhinoceros" *D. simus* (below). In the American Museum of Natural History.

Much time must have elapsed between the first halt in the glacial retreat and the appearance of Magdalenian man in this cave. Boule and Penck agree in saying that the Magdalenian or reindeer man arrived in the Schaffhausen region long after the last Quaternary glaciers had vanished thence, that is, after the disappearance of the tundra fauna.[1]

Kesslerloch Cave. — Similar conclusions result from the study of the geologic conditions surrounding the Kesslerloch Cave of Thayngen in Switzerland (Fig. 176, 37). This famous cave lies on the edge of a moderately wide valley, traversed by a brook.[2] In this sheltered, well-watered, hilly region, woods flourished and harbored the forest animals, at the same time that the glaciers retreating southward left damp and stony areas, closely followed by a tundra fauna. The woolly rhinoceros and the mammoth

[1] Penck, A., Die Glacialbildungen um Schaffhausen und ihre Beziehungen zu den prähistorischen Stationen des Schweizersbildes und von Thayngen. *Neue Denkschr. allg. schweiz. Ges. gesam. Naturwiss.* Vol. XXXV, 1896, pp. 155–179.

[2] Nüesch, J., Das Kesslerloch, eine Höhle aus paläolithischer Zeit. Neue Grabungen und Funde. *Neue Denkschr. allg. schweiz. Ges. gesam. Naturwiss.*, Vol. XXXIX, Pt. 2, pp. 1–72.

persisted longer here than in other parts of Europe. As analyzed by Nüesch, we discover here mammals distinctive of the tundras, of the steppes, of the modern Alps (marmot, chamois, ibex), of the meadow-forests (bison, urus), and finally of the modern forest type (lion, wolf, brown bear, pine marten, squirrel, wild boar, and stag). These mammal zones undoubtedly correspond with the passing or evolution of several human culture stages (perhaps the Aurignacian, Solutrian, and Magdalenian). While the tundra fauna was pushing southward into the heart of Switzerland, it had already vanished from central Germany, Belgium, and France, where it had been superseded by a steppe, or even a meadow-forest fauna. The human artifacts show that these deposits parallel those of Schweizersbild, both belonging to the Magdalenian. A hearth with ashes and coals, and many charred bones of old and young mammals, including the woolly rhinoceros, have been found here. The human remains show that a race of pigmies dwelt here smaller even than the small men of Schweizersbild, their height being estimated at 120 cm. (4 feet).[1] The horse of Kesslerloch shows many resemblances to the Przewalsky horse of the high steppes of Central Asia.[2]

The fauna of *Vöklinshofen*[3] includes a similar intermingling of tundra, steppe, mountain, and meadow-forest types.

The same is true of the scattered deposits[4] in Thuringia near *Saalfeld, Gera, Jena, Leipzig,* etc. The loess fauna near *Würzburg,* Bavaria,[5] also includes twenty species of mammals divided into typically modern tundra forms of northern Asia, typical modern steppe forms of central Asia and Siberia, together with the four characteristic great mammals of the period, the mammoth, the woolly rhinoceros, urus, and bison.

The arctic character of the fauna of *Châteauneuf-sur-Charente*[6] in central France is very conspicuous, most of the species belonging either to the tundras or the steppes of modern Europe. The bones of many young animals occur in this deposit, which may be explained perhaps on the supposition that the animals fell into the fissure while the opening was lightly covered with snow, the young being the most frequently entrapped.

Summary. — This grand fauna is singularly uniform; everywhere it includes the woolly rhinoceros, the mammoth, and the reindeer. Highly characteristic forms, intermingled with these at favorable points, are the

[1] Nüesch, *op cit.*, p. 21.

[2] Studer, T., Die Knochenreste aus der Höhle zum Kesslerloch bei Thayngen. *Neue Denkschr. allg. schweiz. Ges. gesam. Naturwiss.*, Vol. XXXIX, Pt. 2, 1904, pp. 73–112.

[3] Lepsius, R., Geologie von Deutschland und den Angrenzenden Gebieten. Erster Teil, Das Westliche und Südliche Deutschland. Stuttgart, 1892.

[4] Pohlig, H., Vorläufige Mittheilungen über das Plistocæn, insbesondere Thüringens. *Sitzungsber. Niederrhein. Ges. Bonn,* Mar. 3, 1884, pp. 2–15.

[5] Nehring, A., Übersicht über vierundzwanzig mitteleuropäische Quartär-Faunen. *Zeitschr. deutsch. geolog. Ges.*, Jahrg. 1880, pp. 468–509.

[6] Boule, M., and Chauvet, G., Sur l'existence d'une faune d'animaux arctiques dans la Charente à l'époque quaternaire. *C.R. Acad. Sci. Paris,* Vol. XXVIII, 1899, pp. 1188–1190.

bison and the urus. The five grand geographic components of the fauna are the following: the tundra, steppe, alpine, the meadow-forest, the modern forest. All are contemporaneous with Palæolithic man except the modern forest mammals, which belong to the Neolithic age.

Human Culture Stages

Solutrian. — The Solutrian Stage succeeds the Mousterian. According to Penck [1] it represents the maximum of the last glacial advance, the tundra and steppe period of mammalian life. In the opinion of all French archæologists the Solutrian represents the beginning of the Reindeer Period, and is closely joined with the Magdalenian, which represents the close of the Reindeer Period, both being entirely post-glacial. According to Pohlig [2] the Solutrian is not represented in the deposits of England, Germany, Austria, Belgium, or Switzerland. It is typified at Solutré (Fig. 176, 32), in the vicinity of the river Saône, midway between Châlon and Lyon, the site of an open-air palæolithic camp. Toussaint enumerates fragments of at least 100,000 horses, which, mingled with other bones of the chase, formed a sort of rampart around the camp of Solutré. The majority of these horses belonged to the stout-headed, short-limbed 'Norse' or 'forest' type of Ewart, measuring about fifty-four inches (13.2 hands) at the withers, the size of an existing pony. The large joints and hoofs are especially adapted to the low-lying marshy ground in the vicinity of forests and for feeding during part of the year on coarse grasses, roots, and other hard substances, for which its long teeth and powerful jaws were well adapted.[3] There is no evidence that men of the Solutrian age either bred or reared these animals; had they been bred for food, young animals would appear more abundant. The majority of the remains are of horses from five to seven years of age.

Magdalenian. — The Magdalenian Stage belongs to the faunal zone of the last stages of the mammoth, the woolly rhinoceros, and the reindeer. It represents the close of the 'Reindeer Period' of the older classifications. Boule places the Magdalenian well along in the post-glacial period. The mammoth existed in Italy up to Mousterian times, while in France it persisted up to the Magdalenian. Boule and Penck agree that it corresponds with the end of the last glacial epoch, or with the last glacial retreat.[4] It is typified by the upper levels of the rich deposits of Schweizersbild near Schaffhausen, and of the Kesslerloch Cave.

[1] See Penck's Table, p. 379.

[2] Pohlig, H., Eiszeit und Urgeschichte des Menschen. Leipzig, 1907.

[3] Ewart, J. C., The Multiple Origin of Horses and Ponies. *Trans. Highland Agric. Soc. of Scotland*, 1904, pp. 1–39.

[4] Boule, M., Observations sur un Silex Taillé du Jura et sur la Chronologie de M. Penck. *L'Anthropol.*, Vol. XIX, 1908; Penck, A., Lect. before N.Y. Acad. Sci., Jan. 25, 1909.

4. The Fourth, Post-Pleistocene, or Modern Fauna

We now enter the recent, Holocene, or Neolithic age. The mammals of this epoch differ from the three preceding Pleistocene Faunas in the extinction of the mammoth and the woolly rhinoceros, as well as of the cave bear, lion, hyæna, species which left no descendants; and finally in the retreat to the north and northeast of the highly specialized tundra and steppe types.

There remained in the plains and mountains of Europe the forest-meadow, the pure forest, and the alpine types, all direct descendants of the mammals of preceding stages. It is remarkable that no new mammals appear except those introduced by Neolithic man. The fauna of early Neolithic times is directly sequent upon that of late Palæolithic times. This fauna has been discovered in the Swiss lake dwellings [1] (Fig. 176, 38-40) at Moosseedorf, Wauwyl, Robenhausen, Concise, etc. In the peat bogs of Hassleben (41), etc., in the travertines of Jena, Langensalza (42), etc.,[2] have been found the following mammals:

Bison bonasus, the European bison, still surviving in Lithuania.
Bos primigenius, collateral ancestor of the long-horned larger existing cattle of western Europe. The '*urus*,' of Cæsar's text, surviving in Germany until the twelfth century.
Bos longifrons, the 'Celtic short-horn,' the probable ancestor of the small breeds of British short-horned and hornless cattle.
Cervus elaphus, the red deer or stag.
Cervus capreolus, the roe deer.
Alces machlis, the elk or moose.
Rangifer tarandus, the reindeer, surviving in central Europe until the twelfth century.
Cervus dama, the fallow deer, replacing the giant deer.
Capra ibex, the ibex of the mountain or alpine fauna.
Rupicapra tragus, the chamois of the mountain fauna.
Sus scrofa ferus, the wild boar.
Sus scrofa palustris, the turf pig.
Equus caballus celticus, the Celtic pony, representative of the 'plateau' type.
Equus caballus typicus, the Norse, or 'forest' horse.
Castor fiber, the beaver.
Sciurus vulgaris, the common squirrel.
Lepus timidus, the European hare.
Lepus variabilis, the arctic hare, in Ireland and the north.

[1] Rütimeyer, L., Die Fauna der Pfahlbauten der Schweiz. *Neue Denkschr. allg. schweiz. Gesell. gesam. Naturwiss.*, Vol. XIX. Zürich, 1862.

[2] Pohlig, H., Vorläufige Mittheilungen über das Plistocæn, insbesondere Thüringens. *Sitzungsber. Niederrhein. Ges. Bonn*, Mar. 3, 1884, pp. 2–15.

Mus sylvaticus, the field mouse.
Marmota marmotta, the marmot of the alpine fauna.
Ursus arctos, the brown bear.
Meles taxus, the badger.
Mustela martes, the pine marten, also the weasel, pole cat, the ermine, etc.
Lutra vulgaris, the otter.
Gulo luscus, the wolverine.
Canis lupus, the wolf.
Canis vulpes, the fox.
Felis catus, the wild cat.

There is evidence of the 'plateau' or 'Celtic' horse in the Neolithic deposits of Essex and of Switzerland (La Têne); it was widely distributed in Europe and Asia in prehistoric times.[1]

It is beyond the purpose of this volume to trace the history of domestication. The Neolithic immigrants, or men of the New Stone Age, possessed or brought with them cattle, sheep, goats, pigs, horses, and dogs. Appreciating the value of domestication, they certainly captured and domesticated three indigenous European species, namely, the Celtic short-horn cattle, the forest horse (*E. caballus typicus*) and the Celtic horse (*E. caballus celticus*). The wild ox (*Bos primigenius*) was hunted but not domesticated. The domestic ox (*Bos taurus*) shows many points of resemblance to the *Urus*, but is not directly descended from it, but rather from the *Bos trochoceros* type of the Pleistocene of Italy. Rütimeyer has made an exhaustive study of this subject,[2] tracing the origin of the various types of domesticated cattle.

II. PLEISTOCENE LIFE OF NORTH AFRICA

In no region of the world have more profound changes occurred during and since Pleistocene times than in Africa north of the Sahara. In its mammal life this region is now part of Europe, or *Palæarctic;* in Quaternary times it was still more distinctively a part of Africa, or *Ethiopian.* One cannot fail to be struck, observes Boule,[3] with the essentially African character of the Quaternary mammals of Algeria. With the exception of the bear (*Ursus*) every genus still inhabits the dark continent, and several are peculiar to it (*Phacochœrus, Hippopotamus,* the giraffe, and various antelopes). The small number of species common to the Quaternary fauna of Europe and North Africa is noteworthy; the affinity is so slight that it appears that by the middle of the Quaternary, at the latest, communication

[1] Ewart, J. C., *op. cit.*, 1907.

[2] Rütimeyer, L., Die Fauna der Pfahlbauten der Schweiz. *Neue Denkschr. allg. schweiz. Gesell. gesam. Naturwiss.*, Vol. XIX. Zürich, 1862.

[3] Boule, M., Les Mammifères quaternaires de l'Algérie d'après les travaux de Pomel. *L'Anthropol.*, Vol. VII, 1896, pp. 563–571.

between the two continents was interrupted. It is natural to suppose that the lion, hyæna, hippopotamus, now so characteristic of Africa, entered Europe from this North African region, but it appears quite as probable that these animals, all of which occur in the Upper Pliocene of Asia (p. 321), are of Asiatic rather than of African origin. If we adopt this Asiatic theory, we must suppose that during Pliocene times Africa and southern Asia had a great mammalian fauna in common.

The theory of the relative isolation of Africa from Europe in Quaternary times originated with Pomel [1] as a result of his exhaustive review of the entire fauna of North Africa. He concludes that since the resemblances between the European and North African Quaternary faunas are rare and often doubtful, the two continents were separated by the Mediterranean Sea and Straits of Gibraltar then as now.

Climate. — While in Europe the alternating glacial and inter-glacial epochs caused extensive migrations and changes of fauna, Africa was out of the reach of these vicissitudes. It seems well established [2] that after Upper Pliocene times Algeria enjoyed a sub-tropical climate, characterized by abruptly alternating dry and rainy seasons. At the beginning of the Quaternary Period [3] North Africa was probably characterized by excessive rainfall which led to the formation of great alluvial or river and flood plain depositions in the Barbary and Sahara regions.

At this time the mammalian fauna of North Africa, with the exception of some peculiarly Eurasiatic forms (such as the bear, deer, wild boar, and wild sheep) and certain American types (such as the camels), was closely similar to the grand plateau life of equatorial Africa at the present time, including elephants, rhinoceroses, zebras, wild asses, giraffes, wild cattle, buffalo, antelopes, gazelles, gnus, elands, hippopotami, wart hogs, lions, and hyænas. The presence of these animals is consistent with the climatic theory of sub-tropical temperature and alternating dry and rainy seasons.

Various indications point to increasingly long periods of drought and progressive secular desiccation of this great region as the Pleistocene advanced, resulting in the partial extinction and partial migration of the great equatorial life to central and southern Africa. The bear, as a characteristic forest dweller, also became extinct, while the deer, wild sheep, wild boar, and smaller mammals of European type survived to establish for this region its present affinity with Europe.

Sources of African life. — It is premature to attempt to establish the sources of all the various members of this imposing assemblage of mammals; there remains always a great element of doubt which can be eliminated only

[1] Pomel, A., Les Éléphants Quaternaires. *Carte Géol. Algérie, Paléont. Monogr.*, Algiers-1895.

[2] Lamothe, Le Climat de l'Afrique du Nord pendant le Pliocène supérieur et le Pleisto, cène. *C. R. Congr. Géol. Internat.*, Sess. X, Mexico, 1906, Vol. I, 1907, pp. 341–347.

[3] Pomel, A., Les Éléphants Quaternaires. *Carte Géol. Algérie, Paléont. Monogr.*, Algiers, 1895, p. 39.

by discovery of the complete Cænozoic history of Asia and Africa. It would appear probable from our previous studies that several continents contributed to the remote or original ancestry of this fauna, somewhat as follows:

Africa, elephants and mastodons.
Northern Eurasia, deer and bear.
Southern Eurasia, wild cattle and buffalo.
North America, rhinoceroses, various Equidæ, the camel.

The total assemblage may be summarized as follows from Pomel:

Man
Mastodon (Early Pleistocene)
Elephants (several species of African and of *E. meridionalis* type)
Rhinoceroses (2 species of African type)
Hipparions, zebras, and asses
Camels
Giraffes (*Libytherium, Giraffa*)
Deer (of the *Cervus* type)
Wild cattle (*Bos*) (3 species)
Buffalo
Dwarf antelopes, gazelles, gnus, oryx, nagor, elands
Wild sheep
Hippopotami (four species)
Wild boar (*Sus*)
Wart hogs (*Phacochœrus*)
Cave lions (2 species)
Hyænas (spotted and striped)
Bear (of *Helarctos* group)
Jackals
Macaques

Six species of elephants are known, including the mastodon as well as a southern mammoth (*E. meridionalis*) found in the early Pleistocene deposits. In later deposits elephants similar to the *E. antiquus* type of Europe and its dwarf representative in Malta are found, but the most characteristic and widespread form (*E. atlanticus*) belongs to the African sub-genus *Loxodonta*, while differing from the recent African elephant in several points. The latter species (*E. africanus*) only occurs in still more recent deposits of the latest prehistoric period.

Similarly the two species of rhinoceroses (*D. mauritanicus, D. subinermis*) resemble the modern African types, but there is nothing to indicate the existence either of the modern African 'black' or 'white' species. The Pleistocene horses are peculiarly interesting in the alleged survival of several species of hipparions side by side on the plains of Numidia with the early North African horses or zebras. One of the latter (*E. numidicus*) is closely similar to the Upper Pliocene *E. stenonis* of Europe (Boule, 1899).[1] The other (*E. mauritanicus*) shows tooth characters of the recent zebra. Thus there is every reason to believe that in Pleistocene times direct ancestors of the zebra, now confined to equatorial Africa, occupied the extreme north of the continent. To the same period belongs the wild ass, very similar to

[1] Boule, M., Observations sur quelques Équidés Fossiles. *Bull. Soc. Géol. France*, Ser. 3, Vol. XXVII, 1899, pp. 531–542.

the typical African ass (*E. asinus*), which survived in this region until exterminated by the Greeks and Romans, and is now confined to the deserts of Abyssinia.

Among the Artiodactyla the presence of camels (*C. thomasii*) in Palæolithic Pleistocene times and even in deposits of Neolithic age (*C. dromedarius*) is extraordinarily interesting. There is no evidence as to domestication. The earlier of these two camels of ancient Libya had longer legs and was of heavier build than the dromedary. The rare remains of the later form, probably identical with the recent dromedary, may be those of a race which was already emigrating or becoming extinct.[1] The presence of the camel is one of the most convincing proofs of connection of this fauna with that of the Upper Siwaliks of southern Asia, and thus of North America.

Giraffes very similar to the recent African giraffe (*C. giraffa*) have been found in mid-Pleistocene deposits associated with Palæolithic stone implements of the Chellean type.[2] They are also depicted in rock drawings of Neolithic age in Algeria.

In Neolithic times there existed at least one species of deer, whereas at present there are two kinds of deer, the red and the fallow,[3] in North Africa,[3] both undoubted Eurasiatic migrants.

Especially significant of Asiatic and Siwalik affinity are the Pleistocene cattle and buffaloes of North Africa, including contemporary species of *Bos*, all belonging to late Quaternary or to the Neolithic age, partly domesticated, and with remote resemblances to the Pleistocene cattle of France and Spain. Similar Asiatic affinity is found in the remains of buffalo (*Bubalus antiquus*) allied to the existing Indian form. This was a powerful beast which presumably lived in herds, frequenting grassy plains and swampy districts, and in its presence here we seem to find confirmation of what geology teaches us in regard to the dampness of the Quaternary climate. The disappearance of the buffalo from North Africa at the commencement of the Recent Period was no doubt due to the increasingly dry conditions, and partly to destruction by man.

The great number and variety of antelopes is most astonishing in this region, which now is inhabited only by the gazelles (*Gazella*), hartebeest (*Bubalis*), and addax antelope (*Addax*). It includes gnus (*Connochœtes*), several species of *Bubalis* still represented in the Barbary States, an aberrant form (*Oreonagor*), related to the nilgai of India, nine species of gazelles (*Gazella*), the oryx (*Oryx*), the nagor (*Cervicapra redunca*), several large elands (*Oreas*), such as now inhabit South Africa, as well as dwarf antelopes (*Cephalophus*). Beside these plains and desert types of ruminants,

[1] Pomel, A., Caméliens et Cervidés. *Carte Géol. Algérie, Paléont. Monogr.*, Algiers, 1893.

[2] Pallary, P., Note sur la Girafe et le Chameau du Quaternaire Algérien. *Bull. Soc. Géol. France*, Ser. 3, Vol. XXVIII, 1900, pp. 908–909.

[3] See Lydekker, Deer of all Lands. The North African red deer (*Cervus elaphus barbarus*) is smaller than the European race. Evidence on the range of the common fallow deer (*Cervus dama*) in northwestern Africa is not very full.

the hills were covered with wild sheep (*Ovis palæotragus*) very similar to the existing Barbary sheep, as well as goats (*Ovis promaza*).

In the rivers there lived in early and later Pleistocene times a series of species of hippopotami (*H. hipponensis, H. sirensis, H. icosiensis*) leading to a form (*H. annectens*) related to the existing Nile hippopotamus. There

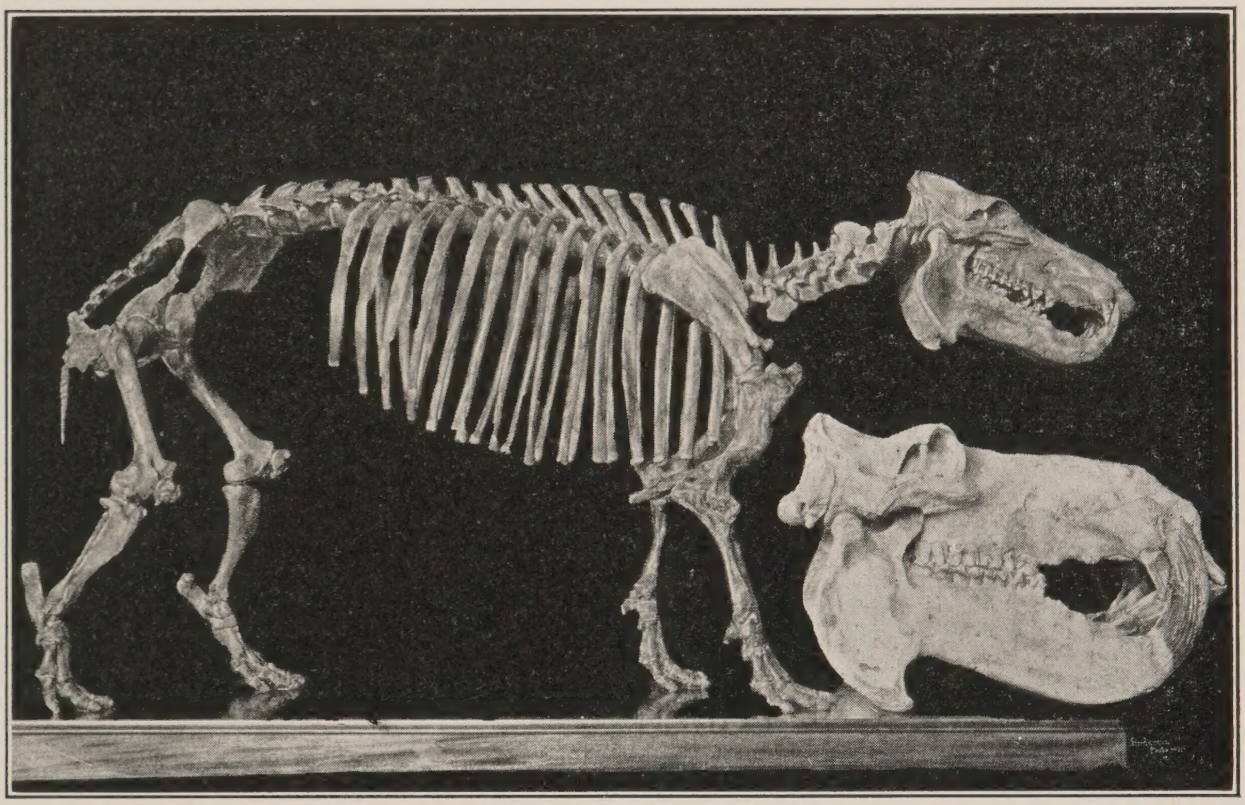


FIG. 186. — Skeleton of the Pleistocene pigmy hippopotamus of Madagascar, *Hippopotamus madagascariensis*, together with a skull of the recent hippopotamus *H. amphibius*. In the American Museum of Natural History.

are also two types of wild boar (*Sus*), and more abundant than these were the wart hogs (*Phacochœrus*) found in the caves and alluvial deposits of Barbary.

Preying upon these Herbivora were lions, leopards, and hyænas, compared by Pomel with Pleistocene cave forms of Europe. The bear (*Ursus libycus*) found fossil in Algeria seems to belong to the *Helarctos* group, now represented by the Malayan sun bear, and possibly derived from the small *U. etruscus* of the European Pliocene. There are also jackals, wolves, the ichneumon, and possibly a polecat.

The primates are represented by a macaque (*Macacus*) not very different from the existing forms which frequent the regions of the Straits of Gibraltar. The prehistoric men of the Barbary States apparently obtained and domesticated the horse, species of sheep, and several dogs, and left many sketches of animals on the rocks of the region.[1]

[1] See Pomel, '93, '94, '95, '96, '97, '98 in Bibliography.

III. PLEISTOCENE LIFE OF NORTH AMERICA

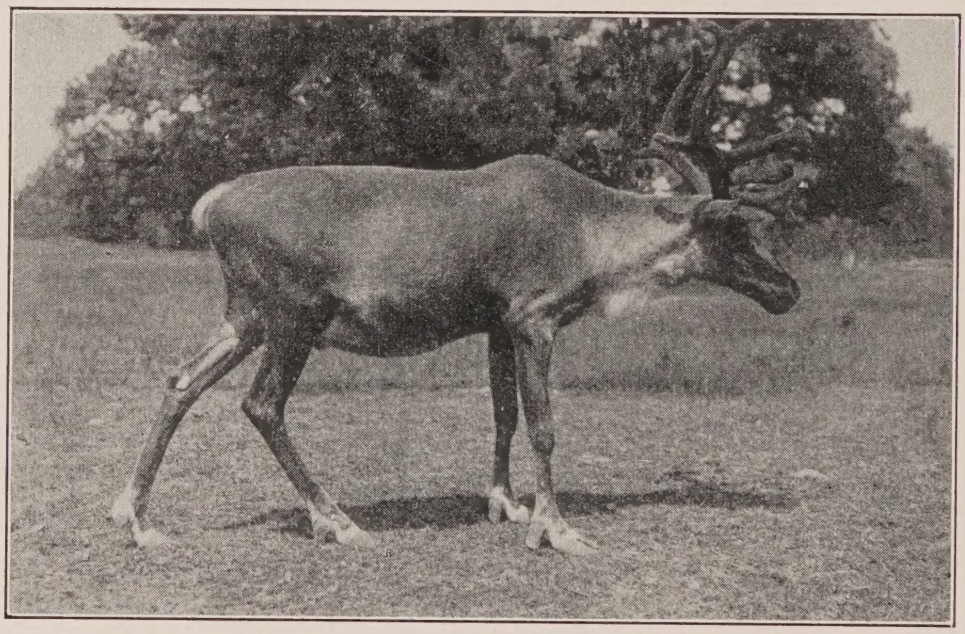
The early and mid-Pleistocene life of North America is the grandest and most varied assemblage of the entire Cænozoic Period on our continent. It lacks the rhinoceroses of Europe, but possesses the mastodons, in addition to an array of elephants more varied and quite as majestic as those of the Old World. Great herds of large llamas and camels are interspersed with enormous troops of horses. Tapirs roam through the forests. True cattle (*Bos*) are not present, but imposing and varied species of bison are widely distributed. An element entirely lacking in Europe is that of the varied types of giant sloths, which were scattered all over the country, as well as the great armored glyptodonts in the South. Preying upon these animals are not only saber-tooth cats, but true cats, rivaling the modern lion and tiger in size.

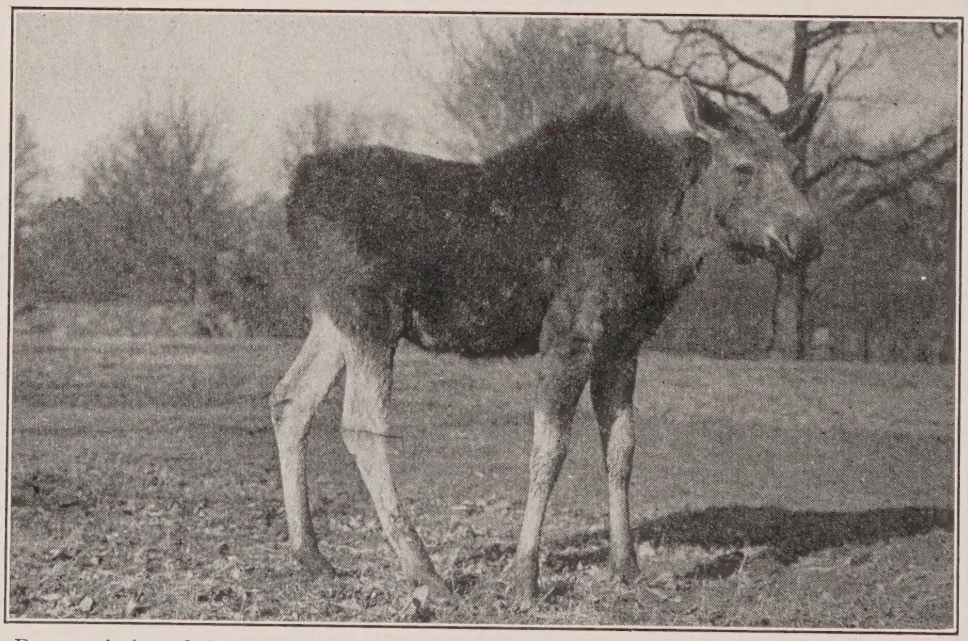
A fact of great importance is that we now witness for the first time the life of the entire United States, of the Plains and Mountain regions of the West, of the Pacific slope, of the vast and hitherto unknown forested stretches of the East, of the sandy savannahs of the South, as well as of portions of British Columbia and Alaska. This more extended range of knowledge enhances both the interest of the subject and its difficulties. When we attempt to correlate the age of faunas east and west of the Sierras and Rocky Mountains, we must consider the influences of these great barriers and of the Pacific Ocean. (See Fig. 194.)

It is true that most of the testimony is of a fragmentary character, but its geographic range and zoölogic diversity are compensating features. The fossil mammals of the East were the first to draw the attention and excite the wonder of the pioneers of American palæontology, of De Kay, Jefferson, Harlan, Couper, and Holmes. It was natural that the discoveries in the Tertiary of the West from the middle of the nineteenth century onward should have diverted attention from the less showy but no less important Quaternary fauna. Leidy, Marsh, and Cope gave it little attention. Quite recently, however, interest has begun to revive, and the studies of Mercer, J. C. Merriam, Sinclair, Furlong, Lucas, Brown, and others are bringing the Quaternary again into its deserved prominence. A thorough-going revision of these mammals and of their environment is still required; for it must be acknowledged that the present review is based upon very incomplete zoölogic and geologic data.

GEOLOGIC DIVISIONS OF THE AMERICAN QUATERNARY

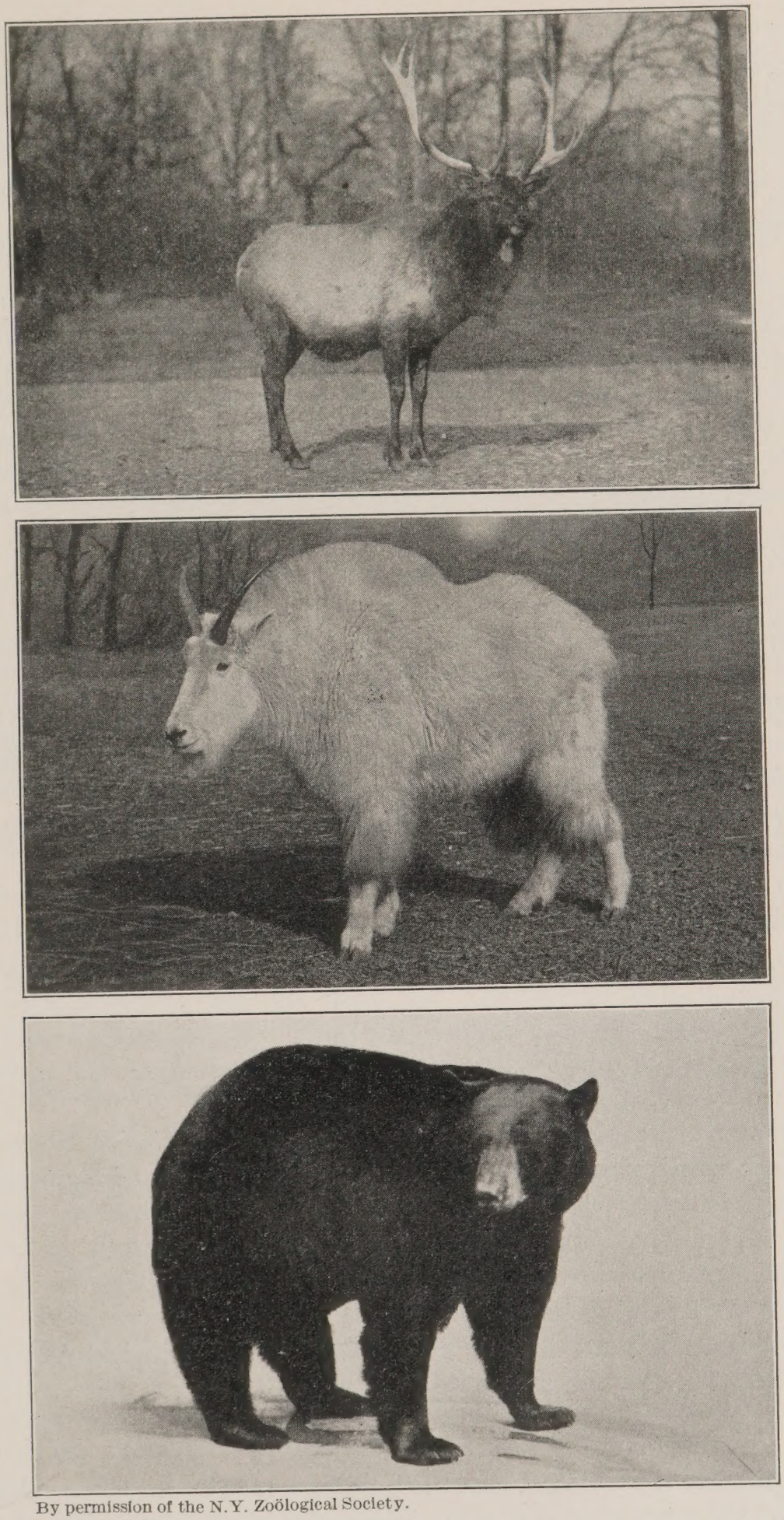
QUATERNARY — AGE OF MAN	II. Holocene or Recent	A moderate elevation of the land where depressed in the preceding period. Mammals of existing species.	7. Champlain Sub-Stage (Marine)
	I. Pleistocene, or Glacial		
	3. Post-Glacial	Depression of lands that were glaciated in the Glacial Period; amelioration of climate; final disappearance of the ice; great river floods and lakes, and fluviatile and lacustrine deposits. Forests and mammals of the temperate zone spread over parts of the previously glaciated regions.	6. Glacio-Lacustrine Sub-Stage
POST-CÆNOZOIC	2. Glacial	Increased elevation of the land over wide regions in higher latitudes; climate in these latitudes of low temperature, abundant precipitation, and consequent production of glaciers. Successive widespread glaciation of the frigid lands, with the exclusion of all life except that of boreal and arctic regions. A subsidence beginning toward the close. Mammals in the glaciated areas preserved in interglacial peat deposits, bogs in glacial moraines, and drift deposits. South of the glaciated areas in caves and in river sands, loess, wind drift and clay deposits.	5a. Wisconsin Glacial, Later 5th *Interglacial* 5. Wisconsin Glacial, Earlier 4th *Interglacial* 4. Iowan Glacial 3d *Interglacial* 3. Illinoian Glacial 2d *Interglacial* 2. Kansan Glacial 1st *Interglacial* 1. Sub-Aftonian Glacial
	1. Pre-Glacial		'Ozarkian Stage' of the Eastern States = 'Sierran Stage' of the Pacific coast.





By permission of the N.Y. Zoölogical Society and Harry C. Whitney (Photo of musk ox).

FIG. 187. — Eurasiatic invaders of North America in the Pleistocene. The musk ox (*Ovibos*), caribou (*Rangifer*), and moose (*Alces*).



By permission of the N.Y. Zoölogical Society.

FIG. 188. — Eurasiatic invaders of North America in the Pleistocene. The wapiti (*Cervus canadensis*), Rocky mountain goat (*Oreamnos*), black bear (*Ursus americanus*).

Faunal Divisions of the Quaternary

The study of the mammals of the Quaternary has by no means progressed so far in America as in Europe; it will be many years before the faunistic succession can be worked out with such chronologic accuracy and precision as has at last been attained by European geologists and palæontologists. The principal difficulty which confronts us in the study of the life of Pleistocene times in America is that the richest deposits of fossil mammals lie to the south of the great terminal moraine, or farthest advance of the glacial cap. In two localities only, the Afton of Iowa and the Toronto Formation of the Don Valley, has it been possible to locate a mammalian fauna between two great series of glacial deposits. Other such localities will doubtless be discovered. Neither are the stages of human culture available, as in the Old World, to supplement and check the time stages of evolution of the mammals. In the meantime, the student must depend upon the following four lines of evidence to mark the progress of Pleistocene time:

First, the *survival* of characteristic Pliocene types, such as the saber-tooths, or machærodonts.

Second, the gradual *extinction* or emigration of these older types, including the greater part of the indigenous large fauna of North America. Thus the saber-tooths, the tapirs, the camels, the horses one by one disappear. Among animals of South American origin the giant sloths and the glyptodonts also gradually vanish. Among forms of Old World origin, the elephants and mastodons gradually disappear. These extinctions, when understood (p. 500), will give us a series of dates.

Third, the gradual *arrival* of types new to America but long resident in the Old World (p. 436–7). Thus we notice the successive arrivals or first records of such Eurasiatic mammals as the moose (*Alces*), the bison (*Bison*), the mountain goat (*Oreamnos*), the musk ox (*Ovibos moschatus*), the true red deer (*Cervus*), the bear (*Ursus*), the reindeer (*Rangifer*), the latter three forms appearing late in Pleistocene times. These arrivals will in time also furnish a series of time divisions.

Fourth, the comparison of the *climatic adaptations* of New World groups with those which prevailed during the four grand zones of mammalian life in Europe which we have described above. Such comparison enables us to give a preliminary outline in somewhat hypothetical form of four great faunistic periods or life zones, broadly analogous to those in Europe, as shown in the following table.

These zones are not sharply distinguishable chronologically at present; they partly overlap and are partly successive.

Hypothetical Division into Four Zones or Faunas, I–IV

The lines of separation between these zones are by no means clearly defined at present, and will depend in the future upon the more accurate definition of species.

I. First or *Equus-Mylodon* Zone of the Plains regions (see p. 452). Mammals of this period include among surviving forms, machærodonts, camels (*llamas*), mylodont sloths, prong-horn antelopes, white-tailed deer, and numerous horses. The glyptodonts survive in the south. The mastodons no longer appear in the Great Plains region. The giant dogs, or

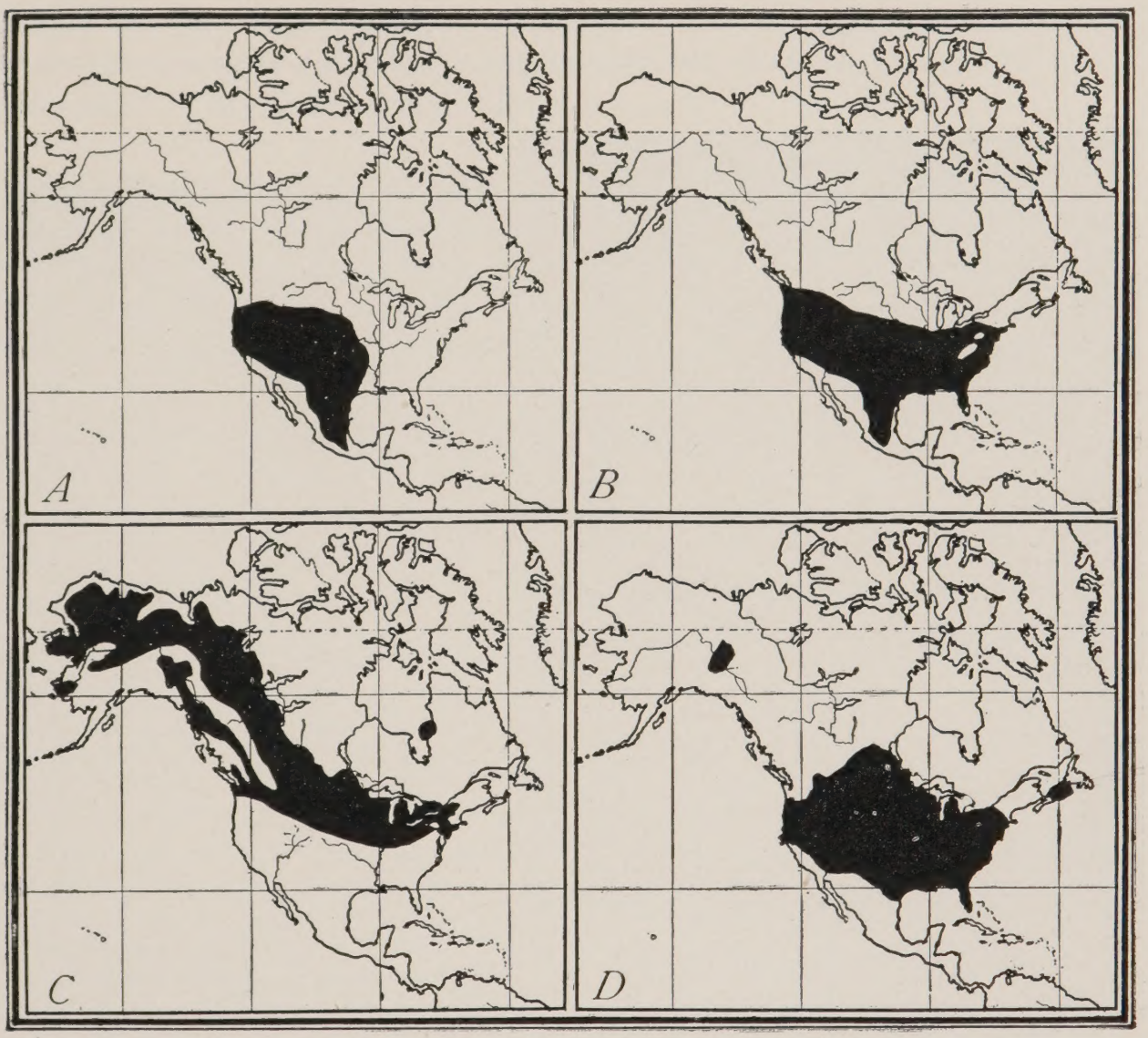


FIG. 189. — Distribution of the Proboscidea in North America. (After Lucas). *A. Elephas imperator*, the imperial mammoth. *B. Elephas columbi*, the Columbian mammoth. *C. Elephas primigenius*, the northern mammoth. *D. Mastodon americanus*, the American mastodon.

dinocyons, appear to survive. The peccaries are represented by *Platygonus*. Among the newly appearing forms are the giant beavers (*Castoroïdes*) and the badgers (*Taxidea*). In this assemblage there are no true European deer (*Cervus*), no bison, no bear, and no mountain goats (*Oreamnos*) nor mountain sheep (*Ovis*), and since it is largely a temperate fauna, there are no reindeer nor musk oxen.

II. Second or *Megalonyx* Zone (see p. 464). The mammals of this stage, which are believed to belong to the temperate and favorable interglacial zones of mid-Pleistocene times and to the south beyond glacial in-

fluences, still include no arctic, tundra, or steppe types. Among the still surviving forms, which, however, disappear during this period, are the machærodonts and the tapirs. The camels, which no longer occur in the east nor in the forested regions, appear to survive in California and in the plateau regions of the southwest. The peccaries are represented by *Mylohyus*. The mylodont sloths seem to have given way gradually to the giant sloths (*Megalonyx*). Giant bisons (*B. latifrons*) abound in the east. Among the rodents the porcupines (*Erethizon*) and the marmots (*Marmota*) appear. Precursors of the musk ox appear (*Euceratherium*). The moose (*Alces*) is frequently recorded, and the true deer (*Cervus*) perhaps arrives very late. There is still no trace of the reindeer (*Rangifer*) nor of the musk ox.

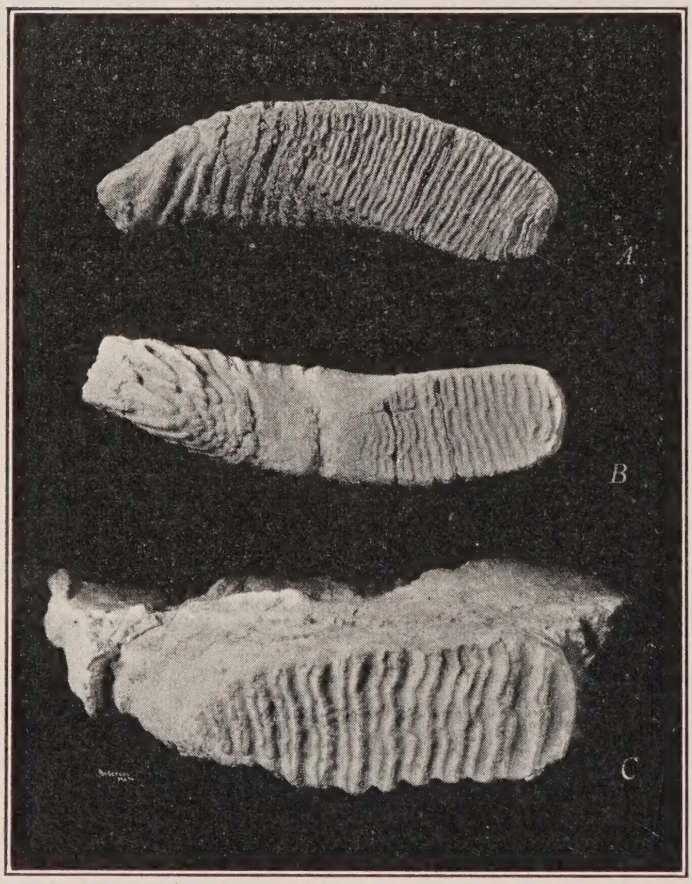


FIG. 190. — Molars of (*A*) the northern mammoth, *Elephas primigenius*, (*B*) the Columbian mammoth, *Elephas columbi*, (*C*) the Imperial mammoth, *Elephas imperator*. In the American Museum of Natural History.

III. Third or *Ovibos-Rangifer* Zone of the plains and forests (see p. 486). The third mammalian fauna is apparently that of the final glacial advance and perhaps of a cold, dry loess period. It includes the musk ox (*Ovibos*), which advances into the Middle States (Fig. 214). The mastodon is the dominant form in the forests of the East. The true northern mammoth (*Elephas primigenius*) appears and spreads as far south as the city of Washington (see Fig. 189, C.). The reindeer (*R. caribou*) is widely distributed in the Middle States. With the remains of the mammoth are associated those of several species of bison. The saber-tooth tigers have disappeared.

IV. Fourth or *Cervus* Zone. The fourth fauna is the prehistoric fauna of the forests of the East and West, of the prairies, and of the great plains and arid region. It is characterized by the very wide distribution of the wapiti (*C. canadensis*), or Old World deer. It includes all the mammals which the early settlers found on this continent. All the horses, tapirs, proboscideans, and other exotic mid-Pleistocene forms have disappeared.

Succession of elephants or mammoths. — The three great elephants of Upper Pliocene and Pleistocene times in North America, although partly

overlapping in time and in range, will probably be found to be characteristic of distinct epochs and habitats, as follows:

3. The northern mammoth (*Elephas primigenius*), ranging from Alaska south to the latitude of Washington. Late Pleistocene, or Zone III.

2. The Columbian mammoth (*Elephas columbi*), ranging from the southerly range of *E. primigenius* to the City of Mexico. Mid-Pleistocene, or Zone II.

1. The imperial mammoth (*Elephas imperator*), ranging from Nebraska to the City of Mexico. Early Pleistocene, or Zone I and (?) II.

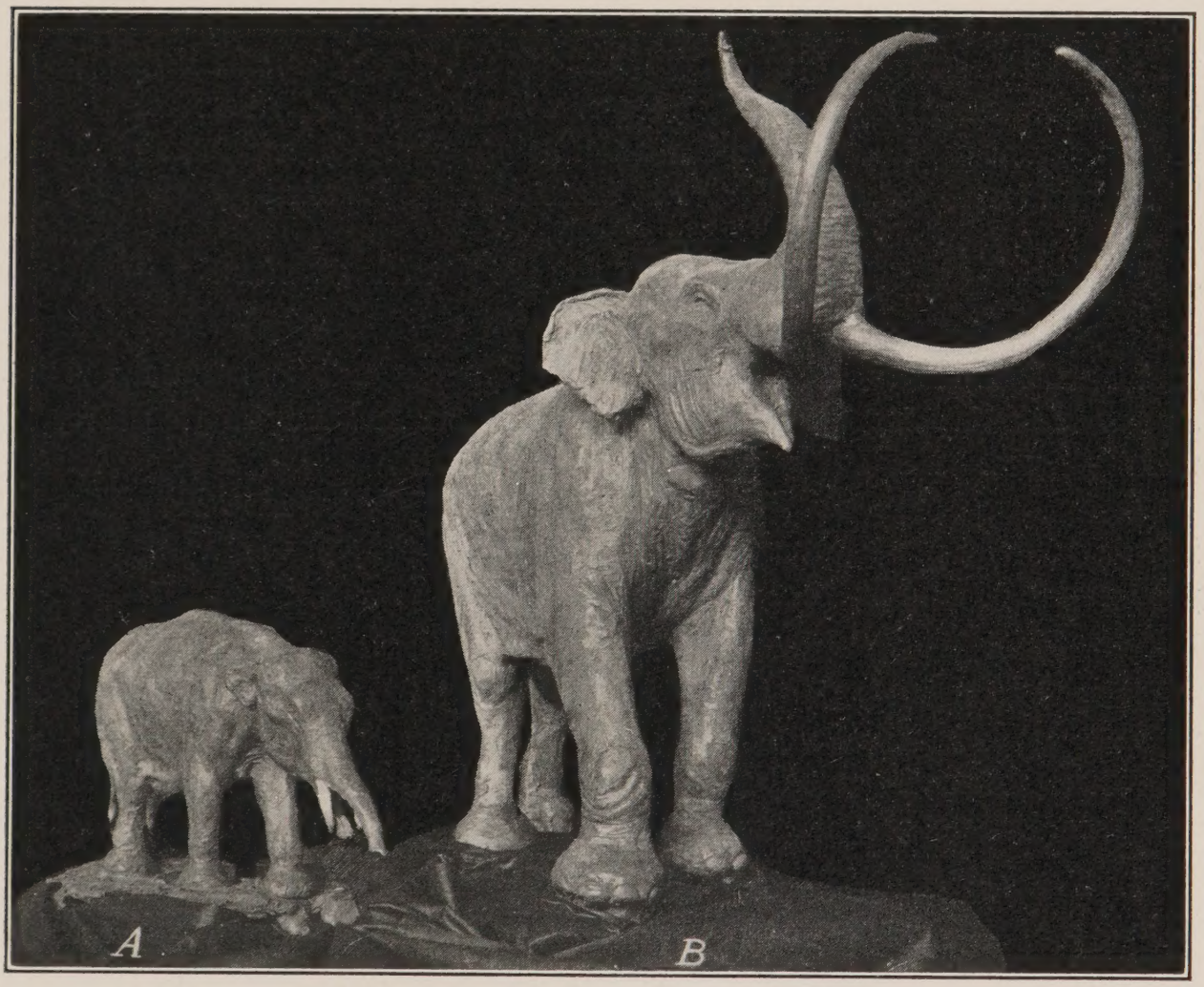


FIG. 191. — Middle Miocene mastodon (*Trilophodon productus*) beside Upper Pliocene or Lower Pleistocene elephant (*E. imperator*). Models by Charles R. Knight in the American Museum of Natural History.

The imperial elephant is an early arrival. It is by far the largest of these animals, attaining a height of over thirteen feet, and more definitely distinguished by the enormous size of its molar teeth, in which the enamel plates are relatively few (seventeen), widely separated, and surrounded by a heavy mass of cement.

The Columbian elephant is an animal of lesser size, attaining a height of eleven feet, with twenty-one to twenty-two cross ridges in its upper grinders.

As in Eurasia, the latest arrival in the latitude of the Middle States is the northern, or hairy mammoth (*E. primigenius*). It is distinguished by its smaller size, its height not exceeding nine feet, by the very numerous (18–27+) and thin plates in its grinding teeth, by its very thick covering of hair and wool.

While the characteristic geographic range of these three elephants, as defined above after the studies of Lucas [1] (Fig. 189), is distinct, there are points where they overlap geographically. Moreover, the teeth of the northern and Columbian mammoths sometimes intergrade, so that it is difficult to distinguish the species. The Columbian and imperial mammoths were for a time at least contemporaneous with the mastodon, because remains of all three species, namely, *E. columbi*, *E. imperator*, and *M. americanus*, have been reported [2] at Afton, Iowa. *E. columbi* and *M. americanus* were contemporaneous through the Central States, Missouri, Indiana, and Ohio. The identification of *E. imperator* in these deposits is somewhat doubtful.

Physiographic and Climatic Changes connected with Continental Elevation and Depression

To understand this life and to sharply demarcate these zones we must survey the series of geographic changes which marked the progress of Quaternary times.

As in Europe, the grand climatic changes of North America were ushered in and perhaps partly caused by great changes of level which altered the proportions of land and sea, and left a whole chain of biotic results in their train. Briefly they were as follows:

ELEVATION, beginning in the Pliocene (see p. 339) and reaching a maximum in late Glacial times.
DEPRESSION, in post-Glacial times.
REËLEVATION, to present levels.

1. ELEVATION. — The seat of the North American glaciers was in British Columbia from three great sources, namely: from eastern (Labradorian), central (Keewatin), and western (Cordilleran) centers. Parts of this region were elevated from 3,000 feet to 5,000 feet (Upham, 1871) above the present level.

Eastern States. — The coast of Maine rose to a height of 1,000 feet, that of southern New England and as far south as Long Island, New York, to 150 feet. Great river channels and fiords were formed along this magnificent coast line, in glacial regions only.[3] See Fig. 214, p. 485.

California. — In early Quaternary times the California coast stood from

[1] Lucas, F. A., North American Elephantids. *Science*, n.s., Vol. XV, no. 379, April 4, 1902, pp. 554–555.

[2] Calvin, Samuel, Present Phase of the Pleistocene Problem in Iowa. *Bull. Geol. Soc. Amer.*, Vol. XX, Mar. 18, 1909, pp. 133–152.

[3] Dana, Manual of Geology, 4th ed., New York, 1894, pp. 946–949.

2,000 to 3,000 feet higher than now; deep cañons were eroded in the Sierra Nevada and Coast ranges; this is the *Sierran Epoch*, which corresponds to the pre-Glacial or *Ozarkian Epoch* of the East. In the succeeding Glacial times the Sierras were covered by a great ice sheet which poured its glaciers down cañons 6,000 or 7,000 feet above sea level. This indicates that in the Glacial Epoch the climate of California was very similar to that which

FIG. 192. — North polar view of the world showing existing outlines, and (dotted areas) elevation to the 200 fathom line, indicating the northern areas of migration in Pleistocene time.

now prevails in the Olympic Peninsula of Washington, where glaciers descend to a point 6,000 feet above sea level. The present climate of this peninsula is cool and rainy, and the forests consist almost entirely of conifers. During this period of elevation the Channel Islands (Santa Rosa) off the coast of southern California were connected with the main land, allowing the mammoths to make their way across on dry land.[1]

[1] Smith, Jas. Perrin, Salient Events in the Geologic History of California, *Science*, n.s., Vol. XXX, no. 767, 1909, pp. 346–351.

Alaska. — The coast of Alaska was elevated, a broad land bridge with Asia existed, and the continental shore line extended far north into the present Arctic Ocean, but the northern portions of the peninsula itself were never covered with ice.

2. Subsidence. — Continental depression was the grand feature of post-Glacial times on both the Atlantic and Pacific coasts. The *San Pedro Stage* of California corresponds with the *Champlain Stage* of the East. In Champlain times a long arm of the sea probably extended up the Hudson River to Lake Champlain, converting it into a small mediterranean sea which attracted seals and even white whales (*Delphinapterus leucas*). The subsidence carried both the North Atlantic and North Pacific shores several hundred feet below their present level. This was a warm and moist climatic period.

3. Reëlevation. — This depression was followed by a renewed elevation, both of the Atlantic and Pacific coasts, which apparently coincided in time with the *Terrace Epoch* of the New England river valleys.

These elevations and subsidences naturally exerted a profound influence (*a*) on temperature, (*b*) on moisture and precipitation, (*c*) on the migrations and extinctions of animal and plant life.

Glacial and Interglacial Stages

Glacial Stages

Wisconsin

Drift from the Keewatin centers. Excessively calcareous. Drift of light yellow color. A moraine-forming ice-sheet covering Iowa. Divided into earlier and later phases.

Iowan

Drift from the northwest Keewatin center barely reaching Iowa. Light yellow in color. Large granitic boulders.

Illinoian

Yellow drift covering small part of Iowa. Ice chiefly from the northeast Labradorian center.

Kansan

Interglacial Stages

Fifth interglacial

Fourth interglacial, PEORIAN

Interval very short as compared with the Yarmouth or Sangamon. Yellow layers containing terrestrial molluscs (*Coccinia pupa*) in the Mississippi valley, in Illinois, in Iowa.

Third interglacial, SANGAMON

Clearly represented in Illinois. Buried forests, peat beds, and pond silts. Forests of tamarack (*Larix*). Long interval, though shorter than the Yarmouth.

Second interglacial, YARMOUTH

Forests and terrestrial faunas typified at Yarmouth. Apparently the longest of the interglacial intervals, "perhaps longer than all post-Illinoian

Kansan

Light blue or gray drift from the northwest, Keewatin center, covering large areas in Iowa. Till, sand, and gravel boulders.

Sub-Aftonian
(=pre-Kansan, Jerseyan, Albertan)

Dark blue or black drift from the northwest, Keewatin center, covering large areas in Iowa. Typical at Afton Junction.

time." Modern mammals: *Lepus sylvaticus, Mephitis mephitica.*

First interglacial, AFTONIAN

Flats, terraces, Aftonian gravels containing fluviatile and terrestrial molluscs. Mammals: *Elephas columbi,* (?) *E. imperator, Mastodon americanus, Equus complicatus, E. occidentalis,* (?) *Cervus,* (?) a cavicorn ruminant. Luxuriant forests of tamarack (*Larix*), peat beds, etc.

This table is partly compiled from the publications of Chamberlin,[1] and will be made more clear by a review of the latest contributions to this subject by Calvin,[2] who observes that within the limits of Iowa the drifting sheets of five distinct glacial advances may be clearly differentiated.

(1) The first is the *pre-Kansan* or *sub-Aftonian* Glaciation, which we may compare with the first or Günz Glaciation of the Swiss Alps. This was followed by a long interglacial interval, known as the *Aftonian* Interglacial Stage, in which the ice disappeared and great floods poured along the drainage courses; especially important is the fact that the Aftonian gravels of Iowa have yielded remains of a rich mammalian fauna (elephants, mastodons, horses, and perhaps moose), which will be described below (p. 467); additional evidence to the same effect is found in the buried forests which extend over practically the whole state of Iowa, in fact, the Aftonian more than any other of the interglacial intervals was a time of luxuriant forest growth; one peat deposit is three feet in thickness. (2) The second or *Kansan* Glaciation may be compared with the Mindel and Saxonian of Europe; the deposits record what appears to have been the maximum phase of the Pleistocene glaciation in Iowa. This was followed by the *Yarmouth* Interglacial Period, which seems to have been the longest of all the interglacial intervals in Iowa; it also was a true interglacial period and had its forests and its terrestrial faunas; the mammals, which are sparsely known, appear to have been partly of modern type. (3) The third or *Illinoian* Glaciation affected directly only a small part of the state of Iowa. This is followed by the third interglacial interval, known as the *Sangamon,* which is indicated by buried forests, pond silts, peat beds containing great quantities of tamarack (*Larix*) roots, etc. Though shorter than the Yarmouth, the Sangamon

[1] Chamberlin, T. C., and Salisbury, R. D., Geology. 8vo, New York, 1905–1906.

[2] Calvin, S., Present Phase of the Pleistocene Problem in Iowa. *Bull. Geol. Soc. Amer.,* Vol. XX, Mar., 1909, pp. 133–152.

interval seems to have been a very long one. (4) This interval was followed by the fourth or *Iowan* Glaciation, of lesser extent, the glaciers stopping a long way short of their predecessors, the Kansan and pre-Kansan, the main body failing to reach the state of Iowa. This was followed by the short Peorian Interglacial Stage. (5) The fifth or *Wisconsin* Glaciation (at some points divided into two, or into early and later Wis-

FIG. 193. — Cox gravel pit near Missouri Valley, Iowa. Showing (*A*) Aftonian gravels overlaid by (*K*) Kansan drift. Photograph by Calvin.

consin stages) sent one ice sheet into Iowa; in general, while not the most extreme, it is the most conspicuous in its results, since it was this last glacial advance which sent the 'great terminal moraine' across the continent.

There is no escape from the conclusion, continues the same author, that the Pleistocene was a long period, compared with which the recent period, or post-Glacial time, would have to be represented by a very small fraction. Even the interglacial intervals, the Yarmouth or Sangamon, exceed the time which has elapsed since the last, or Wisconsin Glaciation, to the present day. According to this view, we may now be living in an interglacial period.

Similar views have recently been expressed by the Canadian geologist, A. P. Coleman.[1] This writer observes that the study of the Canadian interglacial deposits supports the theory that the Ice Age is not a unit, but that in the East it included several glacial periods completely separated by warm periods free from glacial ice. These imply a great complexity and a very long duration for the Pleistocene. The whole epoch must have re-

[1] Coleman, A. P., Interglacial Periods in Canada. *Intern. Geol. Congress.* Mexico, 1906.

quired several hundred thousand years, and the recent times in which we are living may represent only the first third of another interglacial interval. He discusses the two opposing theories in regard to interglacial conditions, namely (1) that the central ice sheet diminished and expanded according to climatic changes, but never disappeared completely until the end of the Wisconsin (or fifth period), (2) that the melting was complete so that the successive sheets represent the work of separate glaciations. The writer adopts the latter view. This is rendered probable by the fact that the rich forest flora and the temperate insect fauna found in beds of the Toronto Formation, corresponding perhaps to the Sangamon or third interglacial interval, indicate that at this interglacial period, at least, eastern North America was entirely free from glaciers and enjoyed climatic conditions similar to the present. This interglacial period alone appears to have lasted from 20,000 to 100,000 years.

Loess. — It is a striking fact that the vast deposits of loess in North America, as in Europe, belong to glacial times, although the loess extends far south of the glacial drift and to the west of the Mississippi River. The aquatic theory of origin has been replaced by the æolian, according to which, while the river floods poured down the materials of the loess these were whipped up by the winds and redeposited on the adjacent uplands, being held after deposition by vegetation. Thus the loess is found along the sides of streams. The deposits seem to be related to periods of aridity.

The thin glacial drift of Nebraska, rarely more than a foot or two in thickness, belongs to the Kansan epoch.[1] The loess bluff deposit, or 'yellow clay' of Nebraska, belonging probably to a later epoch than the 'Kansan,' covers the eastern part of the state, averaging in thickness 100 feet, distributed evenly over hills and hollows alike, and is thus of aerial rather than aquatic origin. It contains remains of the mammoth *E. columbi* and numerous species of terrestrial molluscs.

The geologic conditions in Kansas will be considered in connection with the fauna (p. 461).

Climate of the Great Mountain Basin. — The periodic changes of climate in the mountain region are best recorded in the Great Basin (Fig. 214) between the Wasatch and Sierra Nevada ranges which witnessed the rise and fall of Lake Bonneville[2] the 'greater Salt Lake' of Pleistocene times, and of Lake Lahontan,[3] which lay on the eastern slopes of the Sierras. These fluctuations are of great importance because connected at one point with the *Equus* Zone fauna of Silver Lake in the old Lahontan Lake terraces. The climatic succession is as follows:

[1] Barbour, E. H., Nebraska Geological Survey, Vol. I, 1903. Report of the State Geologist.

[2] Gilbert, G. K., Lake Bonneville. *U.S. Geol. Surv., Monogr.*, Vol. I, 1890.

[3] King, C., Systematic Geology. *U.S. Geol. Explor. 40th parallel*, Clarence King geologist in charge, 1878.

Epochs	*Climate*	*Mammals*
6. Present time Holocene	Infrequent rain, evaporation rapid, dry climate, lacustrine bodies small and varying, no glaciers.	
5. Post-Lahontan (?)post-Glacial	Arid period. Great dryness, average temperature higher than now. Lakes dried up, glaciers melted.	
4. Second rise of Lake Lahontan (?) Period of final glaciation.	More rain than in period 2. Slight evaporation, low temperature, large lakes, and powerful glaciers.	Obsidian spearhead. *Elephas columbi*, *Equus*, *Bison*, (?)*Eschatius*.
3. Inter-Lahontan Period Interglacial	Less moisture, more evaporation, higher temperature. Lakes smaller than at present. Disappearance of glaciers.	
2. First rise of Lake Lahontan (?)First glacial advances	Low temperature, abundant moisture, little evaporation, glaciers on the mountains large, lakes in the valleys.	
1. Pre-Lahontan (?)Pre-Glacial	Dry period, little rain, much evaporation, lakes small, often dried up, mountains without glaciers.	

These periods of moisture are attributed to the southward and northward movements of the *rain-belt*, along the advancing and retreating front of the ice-belt.

At its maximum, Lake Bonneville covered an area of 19,000 square miles, and was 1,000 feet deep, whereas its diminutive descendant, the Great Salt Lake, is less than fifty feet deep. Lake Lahontan covered an area of nearly 9,000 square miles. All lines of physical or erosive evidence point to the shortness of time since the last rise of Lakes Bonneville and Lahontan.

In both basins, *during the period of the second rise*, we have glimpses both of the mammalian life (p. 468) and of the bird life (p. 460), so that it is of the utmost importance and interest to correlate this 'second rise' in time with one of the five epochs of great glacial advance in the central states of Iowa and Illinois. This can only be done through a closer comparison of the specific forms of Pleistocene mammals than has been attained at present.

Migrations of Sangamon flora in Canada. — Deposits on the northern shores of Lake Ontario afford significant evidence of alternate warmer and colder periods respectively in the *Don* and overlying *Scarborough* formations. As in Europe, there are proofs that certain interglacial epochs were

warmer than the present time and that the flora followed the fluctuations of temperature. The plants of the Don Formation on the Don River, near Toronto, Ontario,[1] belong to interglacial times between the Illinoian and the Iowan, or even an earlier stage. The sands and clays of this formation yield a flora of a climate practically similar to that of Virginia, or appreciably warmer than that of Toronto or the northern shores of Lake Ontario at the present time; in fact, it indicates that a temperature as high as that of our Middle and Southern states to-day prevailed as far north as Ontario. It comprises the maple (*Acer*), the judas tree (*Cercis*), the honey-locust (*Gleditschia*), osage orange (*Maclura*), spruce (*Picea*), the hop-hornbeam (*Ostrya*); also plane trees, poplars, plums, oaks, lindens, and elms, forests such as prevail five degrees farther northward.

In these forests of the Toronto Formation, probably belonging between the Illinoian and Iowan ice ages, we also find evidence[2] of the presence of mammoths, mastodons, bison, deer-moose (*Cervalces*), and the reindeer (*R. caribou*).

As proof of migration we discover the cold climate fossil flora of the overlying *Scarborough Beds,* which indicates a return of temperature similar to that of northern Lake Superior or of southern Labrador.

The Leda Clays flora at Green's Creek on the Ottawa (central Canada lat. 46° N.) is boreal rather than arctic.[3] The summer temperature of this period must have been somewhat cooler than at present, probably similar to that of the south coast of Labrador (lat. 51° N.) to-day. The plants from the Leda Clays are still found in some parts of Canada. None of them are arctic.

The most striking proof of southward migration of a northern plant is that of the larch, or tamarack (*Larix*), discovered in Georgia (lat. 34° 30′ N.), or about 480 miles south of its present limit.[4]

Migrations of mammals. — The extreme northward and southward movements of several types of mammals in Pleistocene times along the Atlantic seaboard are also very significant. Our records are chiefly confined to the older observations of Leidy, Weigenmann, J. L. Smith, Cooper, Richardson, Emmons, and Wyman. As an example of the southerly movement of a northerly type, the walrus (*Odobœnus*) migrated as far south as the coast of Georgia. As an example of the northerly movement of a southern type, the manatee (*Manatus*) migrated as far north as the coast of New Jersey. The caribou (*Rangifer*) ranged south into Pennsylvania and Ohio, and we may anticipate the discovery of more southerly records. The moose (*Alces*) is found south of the Ohio and Missouri rivers; the wapiti

[1] Dawson, W., and Penhallow, D. P., On the Pleistocene Flora of Canada. *Bull. Geol. Soc. America*, Vol. I, April, 1890, pp. 311–334; also Penhallow, D. P., Contributions to the Pleistocene Flora of Canada. *Amer. Natural.*, Vol. XLI, no. 487, June, 1907, pp. 443–452.

[2] Coleman, A. P., Letter to the author dated Dec. 18, 1908.

[3] Dawson, J. W., The Geological History of Plants, 1896, pp. 218–271.

[4] Chamberlin, T. C., and Salisbury, R. D., Geology, Vol. III. New York, 1906.

(*Cervus canadensis*) is recorded (F. W. Putnam) as far south as Florida. According to Thompson-Seton [1] the range of the wapiti in prehistoric times did not extend south of the thirty-third parallel (*i.e.* to northern Georgia, Alabama, and Texas).

Migrations of birds in Pleistocene times. — Allen [2] believes that "the Glacial Period left its impress upon the majority of northern birds, through the development in them of the habit of migration, for it is now generally conceded that this habit must have originated in consequence of a great reduction of temperature at the close of the Tertiary. Prior to this period, owing to the comparatively uniform climatic conditions then obtaining almost everywhere, there could have been no necessity for extended periodic movements. During the waning of the ice period the areas offering a congenial summer home to a great multitude of birds became greatly extended, from which, however, they were driven by semi-arctic winters to seek favorable winter haunts farther southward. In this way it is believed the habit of migration has become established as an irresistible hereditary impulse as mandatory as the 'instinct' of reproduction."

The same author speaks elsewhere (*op. cit.*, p. 101) of the "over-crowded tropics." "On account of the flight of all animal life before the successive advances of the great ice sheet there was a crowding together of exiles from the north into the more favored regions to the southward, leading to an intense struggle for existence and a weeding out on a grand scale of forms least fitted for the contest. This period must have been one of great activity in the evolution of new types. Opportunity was given for the gradual adaptation of many forms to lower temperatures than those to which they had been accustomed, and to an enforced change of food. The recession of the ice field at the close of the Glacial Epoch was accompanied by the gradual extension northward of habitable land. A broader area became available in summer than in winter, and an annual migration for a great or less distance on the part of pioneer life became a necessity."

Insect life. — To throw some light on the effect of the Glacial Period on the insect life of North America, Scudder [3] instituted a careful comparison of the number of endemic species in the northern part of the eastern states (*i.e.* the area once covered by the ice sheet) and of the Pacific coast (where it is claimed no ice sheet covered the face of the country), and also to determine how many species were common to north and south, in the East and in the West. If there were found no signs of poverty in the fauna of the regions of former glaciation, we may say that the East has fully recovered from the shock of the Glacial Period. The beetles (*Coleoptera*) were chosen

[1] Thompson-Seton, E., The Wapiti and his Antlers. *Scribner's Magazine*, Vol. XXXIX, no. 1, Jan., 1906.

[2] Allen, J. A., The Geographical Origin and Distribution of North American Birds, Considered in Relation to Faunal Areas of North America. *The Auk*, Vol. X, no. 2, April, 1893.

[3] Scudder, S. H., The Effect of Glaciation and of the Glacial Period on the Present Fauna of North America. *Amer. Jour. Sci.*, Vol. XLVIII, Sept., 1894, pp. 179–187.

as subjects of illustration, since they are at least as sensitive tests of the economic or faunal changes as any other group of animals.[1] Scudder's results show "that on the whole the fauna of the East has nearly or quite recovered from its enforced removal from the northern states and Canada at the time of the Glacial Period, and that whatever influence the past existence of a Glacial Period may now exert upon the distribution of animal life in North America should be sought only in minor features, such as the remnants of *boreal faunas* lingering in favorable spots amid temperate surroundings and the similar features introduced by the latitudinal trend of our great mountain chains."

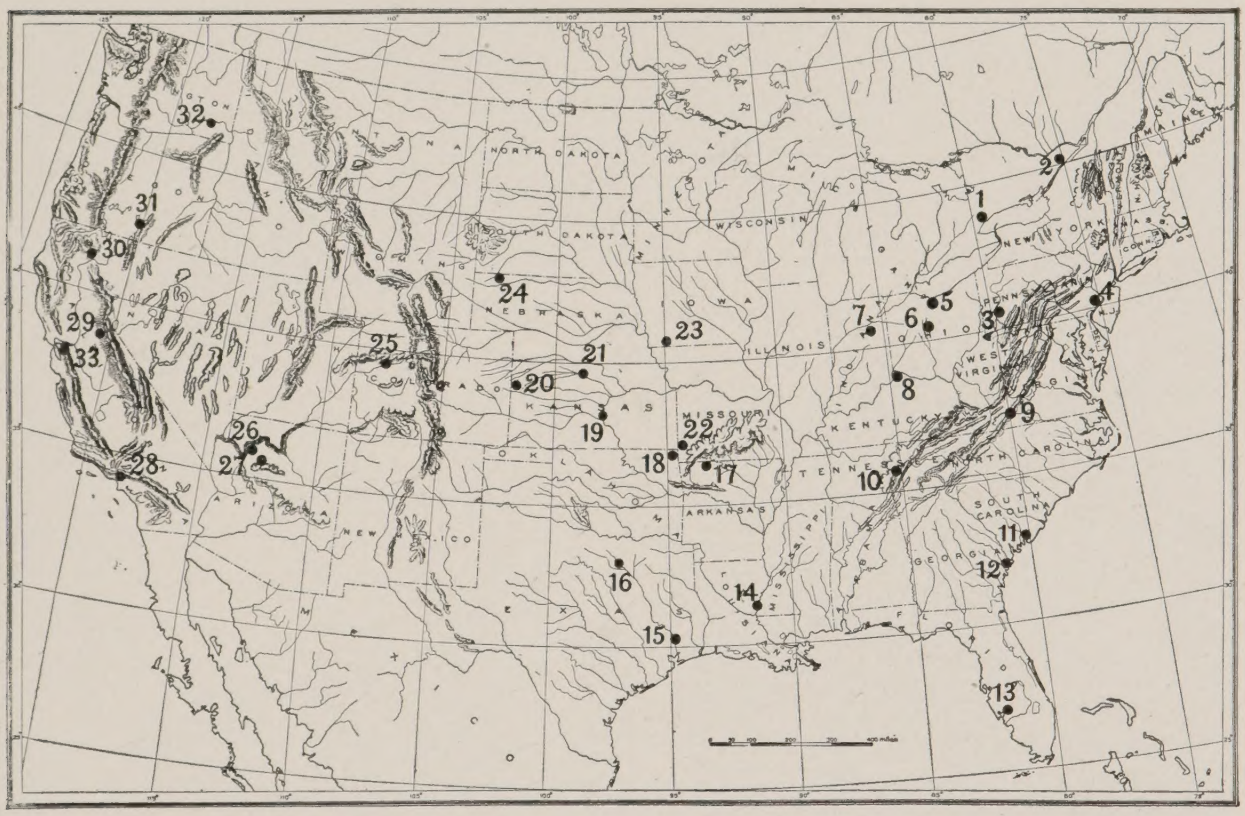


FIG. 194. — **Chief Pleistocene fossil mammal localities of North America.** CANADA. — **1** *Don Valley*, near Toronto. **2** *Iroquois Beach*, Ontario. UNITED STATES. — **3** *Frankstown Cave* (Blair County), **4** *Port Kennedy Cave* near the Schuylkill River, Pa. **5** *Erie Clays*, on Lake Erie near Cleveland, surface muck near **6** *Ashley*, Ohio. Surface muck and gravel near **7** *Jonesboro*, *Merion*, and *Fairmount*, Indiana. **8** *Big Bone Lick* (Boone County), Ky. **9** *Wythe County*, Va. **10** *Big Bone Cabin* (Van Buren County), Tenn. **11** *Ashley River*, near Charleston, S. C. **12** *Skidaway Island*, Ga. **13** *Peace Creek* (Manatee County), Fla. **14** *Natchez*, Miss. **15** *Hardin County*, **16** *Rock Creek* (Parker County), Tex. **17** *Conard Fissure*, near Harrison, Ark. Sulphur spring near **18** *Afton*, Ind. Ter. **19** *McPherson County*, **20** *Twelve Mile Creek*, *Sternberg's Elephant Bed* (Logan County), **21** *Solomon Valley*, Kan. Caves in zinc mines near **22** *Carthage*, Mo. Gravels near **23** *Afton*, Ia. **24** *Hay Springs*, Neb. **25** *Glenwood Springs*, Col. **26** *Anita Mine*, near the Grand Cañon, **27** *Keam's Cañon*, near Holbrook, Ariz. Asphaltum of **28** *Rancho La Brea*, near Los Angeles, **29** *Mercer's Cave*, (Calaveras County), **30** *Potter Creek Cave* and *Samwel Cave* (Shasta County), Cal. **31** *Fossil Lake*, near Silver Lake, Oreg. **32** *Washtucna Lake* (Franklin County), Wash. Alluvial sand, etc. of **33** *San Pablo Bay*, Cal.

[1] Incidental reference may be made at this point to the fact that in the Scarborough Beds of the Toronto interglacial deposits, Ontario, among seventy-eight species of animals seventy-two are beetles.

1. Early and Mid-Pleistocene Mammals of the Plains Regions. The First or Equus Zone Fauna

This is chiefly a plains, desert, and river-border fauna, including some very large mammals, but less varied in type than that of the *Megalonyx* Zone. It begins in early and extends into mid- and perhaps late Pleistocene times.

The life of the plains and mountain regions, or of what may be called the *Equus-Camelus-Mylodon* Zone, is known in numerous and widely scattered deposits in the Great Plains, in the mountain region, and along the

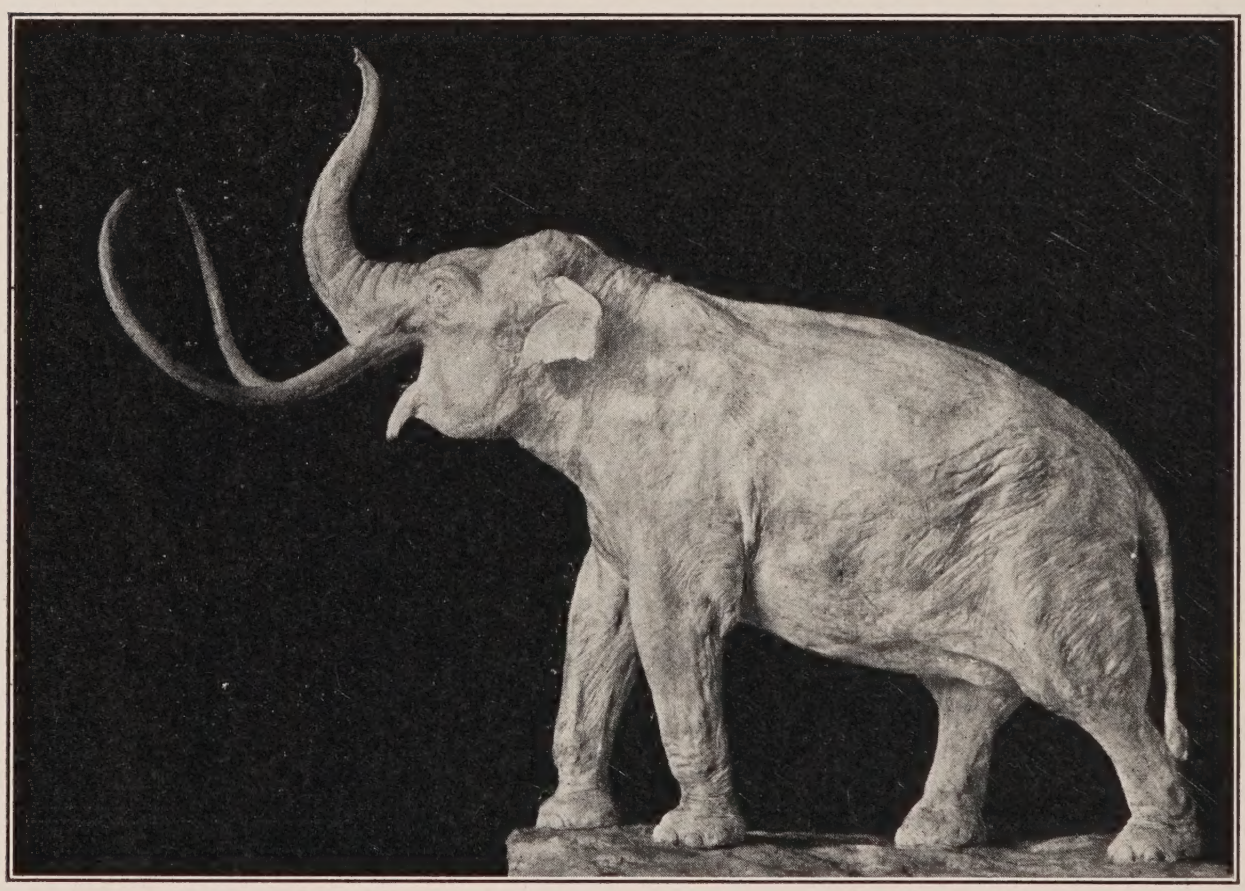


Fig. 195. — The Upper Pliocene or Lower Pleistocene imperial mammoth (*Elephas imperator*). Model by Charles R. Knight in the American Museum of Natural History.

coast of Florida. Some of these local river or wind-drift deposits have received distinct formation names, such as the 'Sheridan' of Scott, the 'Rock Creek' of Gidley.

As we should expect in deposits bordering on great grassy plains and uplands, one of the most abundant mammals is the horse; consequently these formations have come to be known collectively as 'Equus Beds' (Marsh) or the 'Equus Zone.' It is not shown that they are all of the same age; on the contrary, they probably represent a very long period of time. Some may have been deposited near the beginning of the Pleistocene; others may be mid-Pleistocene. We may, therefore, distinguish the 'early' and the 'late' Equus Zone; distinct zonal names will in time be applied.

Thus it must be stated at once that portions of the Equus Zone fauna of the Great Plains region are probably synchronous with the Megalonyx Zone fauna of the forest and mountain region.

Some of the chief localities where the early and mid-Pleistocene mammals of these two epochs have been found together in large numbers are the following, placed in *ascending* order:

6. Kansas Pleistocene, several localities, early and late (Fig. 194, 19, 20, 21).
5. Lake Lahontan (Nevada), Lake Bonneville (Utah) 'upper terraces' (Fig. 214, L, B).
4. Silver Lake, Lake County, Oregon, a more recent phase containing plains and river, or fluviatile types (Fig. 194, 31).
3. Rock Creek, Tule Cañon, Llano Estacado, Texas, a fluviatile formation containing *Equus scotti* (Fig. 194, 16).
2. Hay Springs, western Nebraska, chiefly an open plains and river border fauna (Fig. 194, 24).
1. Peace Creek, southern Florida (see p. 367), a forest and plains fauna of late Pliocene or early Pleistocene times, partly intermingled with a more recent fauna (Fig. 194, 13).

Relative age of the Equus and Megalonyx faunas. — The *late Pleistocene age* of the Silver Lake fauna of the Equus Zone is supported by the geologic and physiographic studies of Gilbert in the region of the great Pleistocene lakes of Bonneville and Lahontan. Cope [1] believed (1895) that the fauna of the Equus Zone, covering areas in Oregon, Nevada, California, Nebraska, the Staked Plains, in southern Texas, Chihuahua, and the valley of Mexico, was throughout contemporary with the Megalonyx fauna of the East, differing from it only in details. He regarded the Megalonyx fauna as pre-Champlain.

This conclusion was accepted by Williston in 1897,[2] who was, moreover, disposed to relegate the Equus fauna to very *late* Pleistocene times. "Every fact furnished from Kansas seems to substantiate Cope's conclusions that the Megalonyx fauna of the East and the Equus fauna of the West were contemporaneous, and that both occurred during the period of depression, that is, during late Pleistocene time." It is certain that during the Champlain period there was a depression in Kansas, though probably not a very profound one. The Champlain is a period of fluviatile conditions and ameliorated climate, of luxuriant forest growth, and more or less submergence. From the presence everywhere, the same author continues, in the

[1] Cope, E. D., The Antiquity of Man in North America. *Amer. Natural.*, Vol. XXIX, no. 342, June, 1895, pp. 593–599.

[2] Williston, S. W., The Pleistocene of Kansas. *Univ. Geol. Surv. Kansas*, Vol. II, 1897, pp. 299–308.

Quaternary deposits of Kansas of *Elephas* [*columbi*] *primigenius* remains, the characteristic species of the Equus Zone, the conclusion is that the prevailing superficial deposits belong to this formation. The author concludes by regarding the Pleistocene mammals of Kansas as probably contemporaneous.

There are many reasons, however, why we should consider certain deposits of the Equus fauna as earlier than the Megalonyx fauna. When we compare the mammals found at Hay Springs, northwestern Nebraska, Rock Creek, Texas, Silver Lake, Oregon, and Peace Creek, Florida, we find many points of similarity, such as the association of many mammals which do not appear together in later formations, and the absence of others which have apparently not yet reached America.

The solution undoubtedly is that the so-called 'Equus Zone' faunas in different localities are not synchronous, but represent an enormously long period of time, some of early and some of mid-Pleistocene age, some preceding and some contemporaneous with the 'Megalonyx Zone' faunas. The 'Equus Zone' is accordingly divided here into (1) early phases, p. 454, and (2) late phases, p. 461.

(*1.*) *Early Phases of the Equus Zone*

These early phases are apparently distinguished by the presence of true camels and by the absence of bison (*Bison*). Contradictory to this statement is the fact that *Bison* is recorded at Peace Creek.

The western and southwestern plains life of the early phase may be summarized as follows:

Horses, very abundant and characteristic.
True camels, as well as llamas, abundant in the west and southeast.
Columbian mammoths, abundant.
Imperial mammoths, not certainly determined in the north, probably present in the south.
The earliest prong-horn antelopes (*Antilocapra*), abundant on the Great Plains.
The last of the merycodonts (*Capromeryx*).
Peccaries of the genus *Platygonus*, not *Dicotyles*.
Mylodont sloths (*Paramylodon*), abundant in the west and southeast.
Glyptodonts, or armored edentates, in the south.
The giant beaver, *Castoroïdes*, making its first appearance.
The badger, *Taxidea*, first appearing.
Machærodonts, or saber-tooths, very numerous.
No other large felines.
Dinocyons, or amphicyonine dogs, doubtfully present.

Mammals absent or undiscovered in this Fauna:

Mastodon, probably abundant in the forests of the east.
Giant sloths (*Megatherium, Megalonyx*), not recorded.
Bison, or buffalo, recorded only at Peace Creek, Florida.
Bear, not recorded at any point.
Mountain sheep, not recorded, a mountain type.
Mountain goat, not recorded, a mountain type.

Of these animals, the most characteristic are the Columbian mammoths, camels, horses, mylodonts, peccaries of the genus *Platygonus*, the giant beavers (*Castoroïdes*). The imperial mammoth (*E. imperator*) is not found

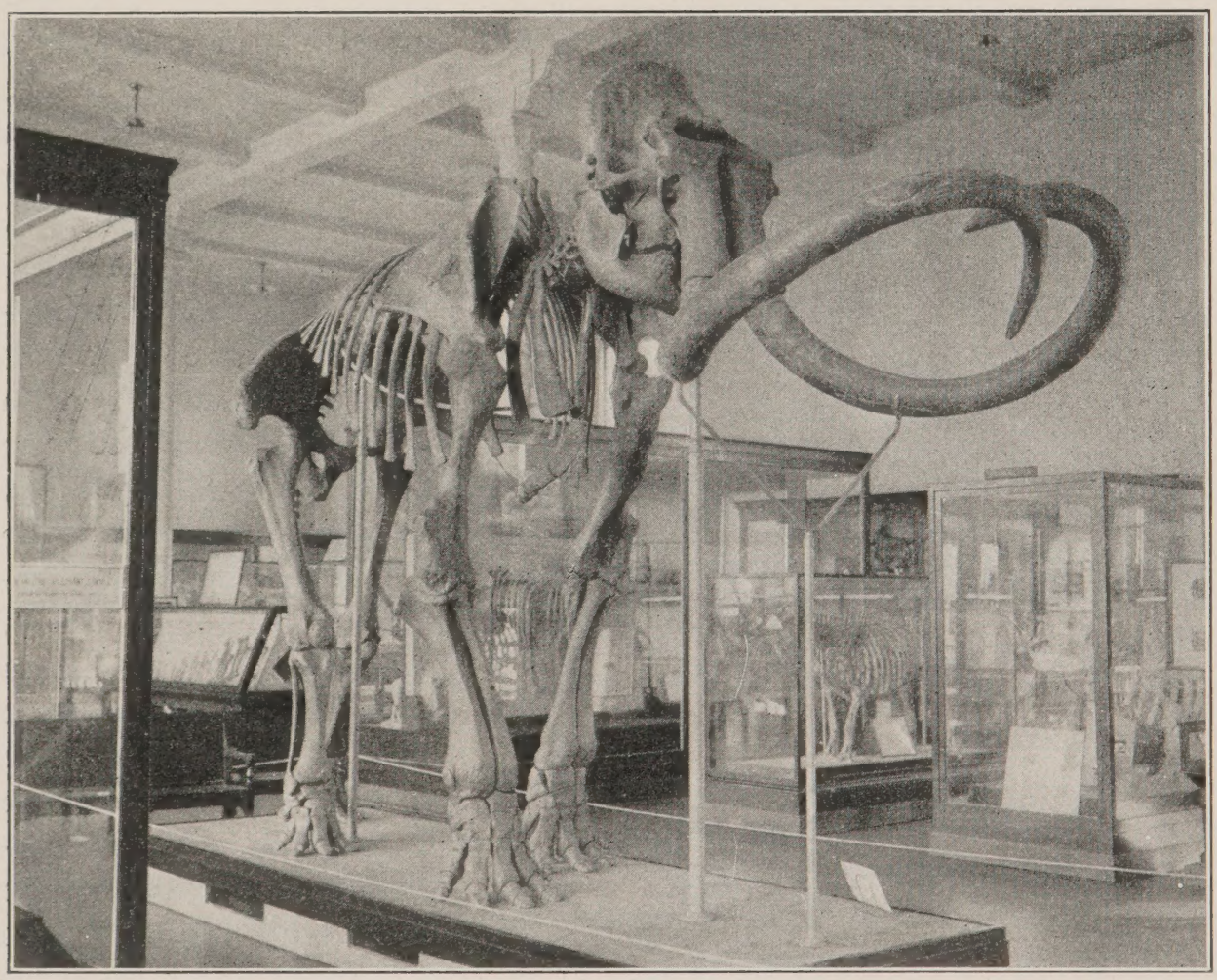


FIG. 196. — Skeleton of the Columbian mammoth *Elephas columbi*, from the Pleistocene of Indiana. In the American Museum of Natural History. After Osborn.

at Hay Springs, Silver Lake, Rock Creek, but is doubtfully reported at Afton, Indian Territory, in association with the Columbian mammoth. Its chief distribution is in the southwest.

The tapir is not found in these western deposits, because they chiefly include the plains fauna, but it was undoubtedly widely distributed in forested regions. Matthew[1] has pointed out the prevalence of plains-

[1] Matthew, W. D., List of the Pleistocene Fauna from Hay Springs, Nebraska. *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI, 1902, pp. 317–322.

living types at Hay Springs, at Silver Lake, and in the Oregon desert, while the more recent fauna of Washtucna Lake, Washington, shows a large proportion of forest and mountain types and no aquatic mammals.

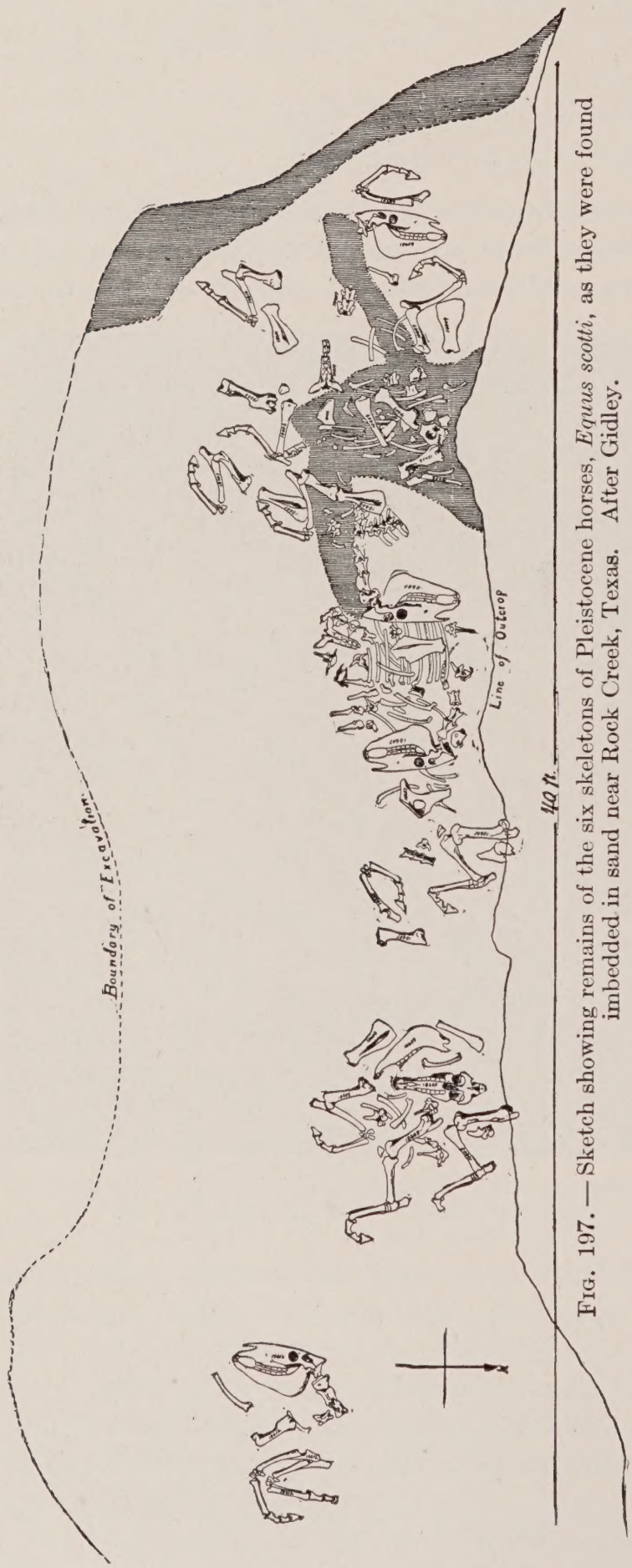


Fig. 197. — Sketch showing remains of the six skeletons of Pleistocene horses, *Equus scotti*, as they were found imbedded in sand near Rock Creek, Texas. After Gidley.

Hay Springs, Nebraska. — The Hay Springs (Fig. 194, 24) fauna, as explored by the American Museum expeditions of 1893 and 1897, is a very rich one and may be taken as typical of the early phase of the Equus Zone. It includes the llama-like cameloids (*Camelops*) and a true camel (*C. americanus*). The true prong-horn antelopes (*Antilocapra*) make their first appearance here, and with them are associated the smaller *Capromeryx* (*C. furcifer*), an animal intermediate between the merycodonts (see pp. 294–5, 357) and the true American prong-horns. The most abundant species of horse is *E. complicatus*, while *E. fraternus*, a smaller animal, is also found. The sloth which appears here is distinct from the mid-Pleistocene *Mylodon harlani* of the East, and according to the determination of Brown belongs to a distinct genus, *Paramylodon*.[1]

[1] Matthew, W. D., List of the Pleistocene Fauna from Hay Springs, Nebraska. *Bull Amer. Mus. Nat. Hist.*, Vol. XVI, 1902, pp. 317–322.

Paramylodon is described [1] as in some features more, in others less specialized than Mylodon and retaining features of the older, more primitive sloths. It differs from Mylodon in having but four upper teeth, the hindermost of which is tri-lobed instead of bi-lobed. The limbs are more slender and the ankles more flexible than in Mylodon. A second specimen has recently been found [2] near Walsenburg, Colorado, which contains five upper teeth, and while exhibiting the elongate skull and inflated muzzle of the type of *Paramylodon*, it indicates that the generic distinction between these two forms may be insecurely founded. A fine specimen of a Mylodon,

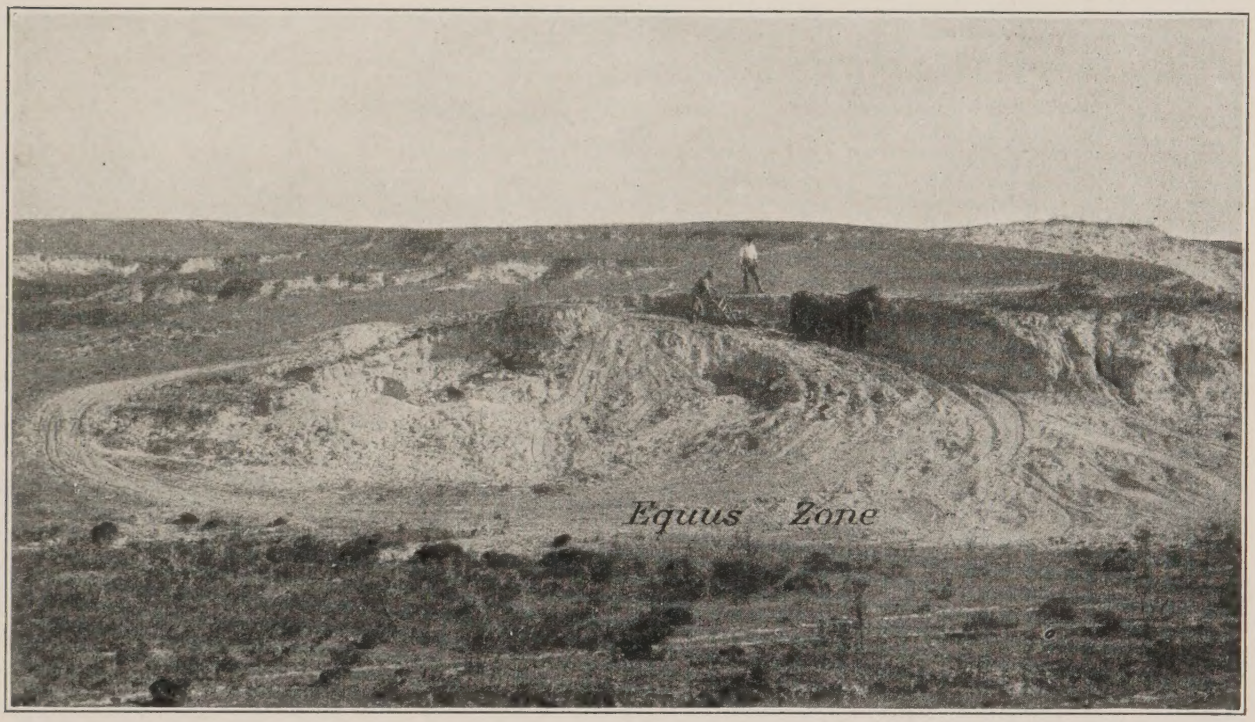


FIG. 198. — Quarry in which six skeletons of the Lower Pleistocene horse *Equus scotti* were found. Head of Rock Creek, Texas. Lower Pleistocene or Equus Zone. Photograph by American Museum, 1900.

not distinguishable from the Walsenburg specimen, comprising most of the skeleton, was found in 1880 by Mr. S. Garman of a Harvard University expedition at Hay Springs. A description of this specimen, now preserved in the Museum of Comparative Zoölogy, has not been published.

Prairie wolves (*C. latrans*) have been found, but few if any true felids. The peccaries (*Platygonus*) are much more swift-footed and advanced in dentition than the modern peccary, and may be supposed to have lived more in the open. The prairie dogs (*Cynomys*), gophers (*Thomomys*), and field mice (*Microtus*) are even now characteristic of the plains of this same Nebraska region, while muskrats (*Fiber zibethicus*) occurred then as now along the streams. Remains of a small species of *Castoroïdes* are occasional. This fauna is, on the whole, similar to that of Silver Lake, which differs

[1] Brown, Barnum, A New Genus of Ground Sloth from the Pleistocene of Nebraska. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIX, Art. xxii, Oct. 28, 1903, pp. 569–583.

[2] Cockerell, T. D. A., A Fossil Ground-Sloth in Colorado. *Univ. Col. Studies*, Vol. VI, no. 4, Boulder, Col., June, 1909, pp. 309–312.

from it in the presence of the beaver (*Castor*) and the otter (*Lutra*), which are not found at Hay Springs.

Rock Creek, Texas. — (Fig. 194, 16.) These beds are extensively exposed in the Staked Plains of Texas (Fig. 166) along the south side of Tule Cañon. As described above (p. 362), they represent a Lower Pleistocene river channel cutting its way into an older Miocene horizon. They are especially famous for the magnificent series of six skeletons of horses discovered by Gidley [1] in 1900 and referred to *Equus scotti*. (See Figs. 197 and 198.) In these beds are also found a peccary (*Platygonus*) and the

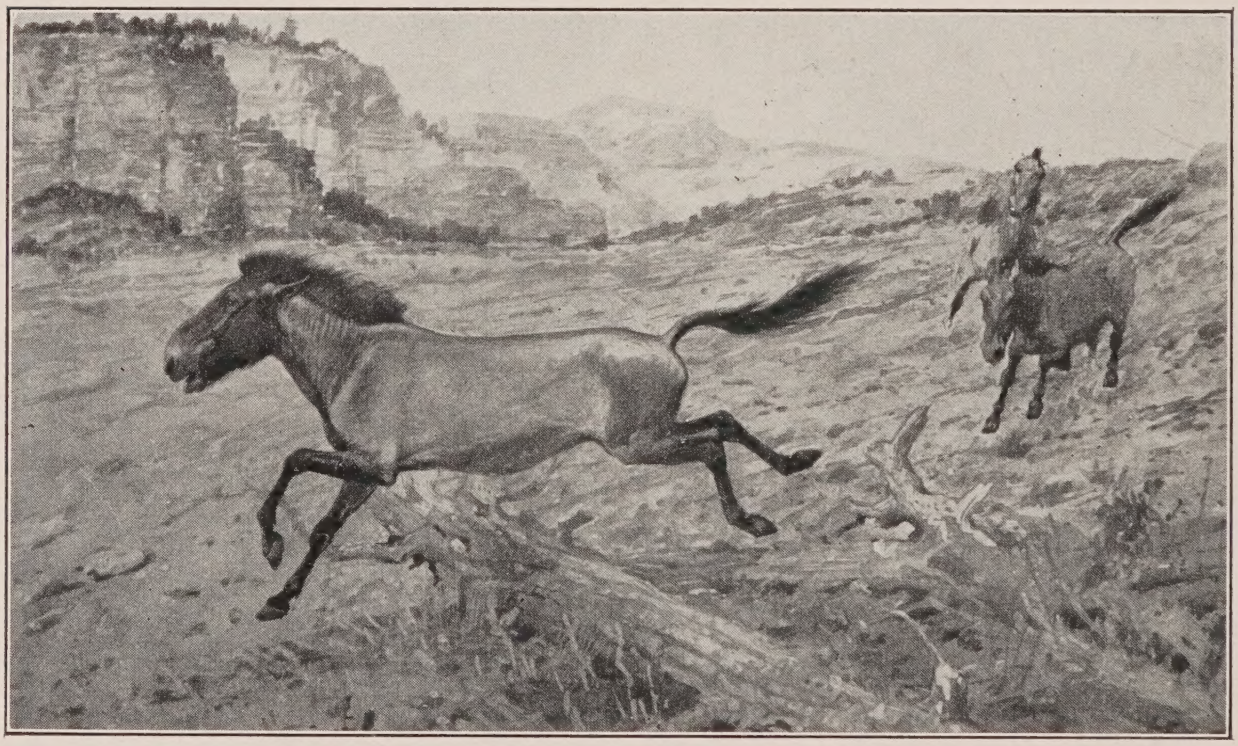


Fig. 199. — The Lower Pleistocene true horse of Texas, *Equus scotti*. After original by Charles R. Knight in the American Museum of Natural History.

imperial mammoth (*E. imperator*). Cope [2] had previously reported from Rock Creek a sloth (*Mylodon sodalis*), several species of horses, and two cameloids (*Holomeniscus sulcatus, H. macrocephalus*), as well as two large land tortoises.

Silver Lake of the Oregon Desert. — (Fig. 194, 31.) One hundred and fifty miles northwest of the old Lahontan shore lines in the heart of the Oregon desert of the Great Basin, and twenty miles northeast of Silver Lake there is a slight depression in the desert perhaps twenty acres in extent marked Christmas Lake on the maps, to which Cope gave the name "Fossil Lake." This 'Silver,' 'Christmas,' or 'Fossil' lake region was succes-

[1] Gidley, J. W., A New Species of Pleistocene Horse from the Staked Plains of Texas. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIII, no. 13, pp. 114–116; also Tooth Characters and Revision of the North American Species of the Genus *Equus*. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIV, Art. ix, 1901, pp. 134–137.

[2] Cope, E. D., Report of the Geological Survey of Texas, 1892, 1893, p. 87.

sively explored by Condon, Cope, Sternberg (who made the chief collections), and Russel (1882). It now presents a perfectly dry surface consisting of a light-colored mixture of sand and clay or dried mud of volcanic origin; all the fossils lie in this last friable deposit of volcanic dust. Though actually twenty miles distant from Silver Lake, the rich fauna of mammals and birds found has been described by Cope[1] and Shufeldt, and referred to by Gilbert, as the fauna of the Silver Lake Equus beds. It is obvious that we have no means of correlating it in time with the lacustral movements either of Lake Bonneville or of Lake Lahontan, and that at present the correlation of this fauna with either of the phases of the Glacial Epoch will be impossible unless shore lines of the Silver or Christmas Lake region admit of investigation similar to that which has been so successful in the great ancient lakes to the south.

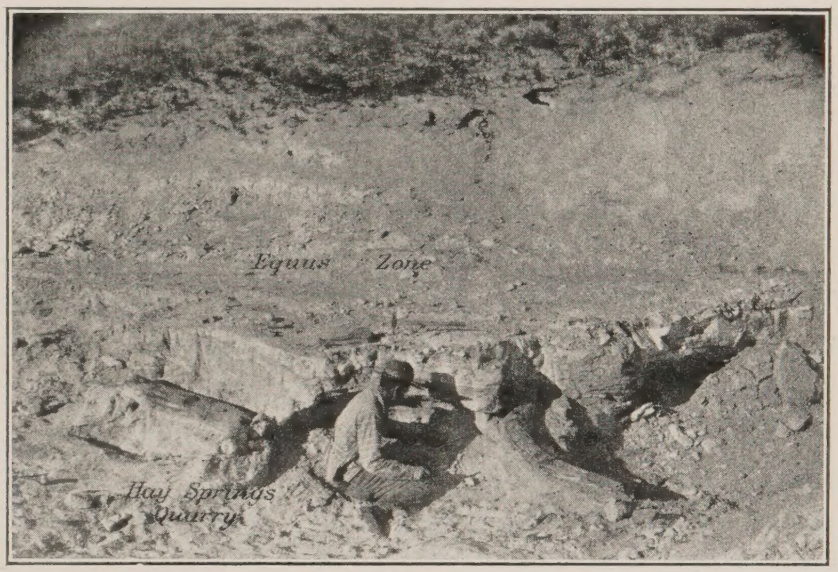


FIG. 200. — The famous Hay Springs Quarry of western Nebraska in the Equus Zone, Lower Pleistocene. Photograph by American Museum of Natural History expedition of 1897.

The Silver Lake mammal fauna appears to be slightly younger or more recent than that of the Hay Springs Equus beds above described; both the camels and horses are somewhat more progressive in type. It is noteworthy that the bison does not occur in this rich fauna.

We owe to Cope[1] (1889) and Shufeldt[2] (1892) peculiarly picturesque descriptions of this region as it may have been in Pleistocene times.

Proof that the country was partly fluviatile and partly wooded is afforded by the presence of the muskrat (*Fiber*), the otter (*Lutra*), the beaver (*Castor fiber*), and the giant beaver (*Castoroïdes*). The supposed great mylodont sloth (*Mylodon sodalis*), an animal as large as the existing grizzly bear, also affords evidence of forested conditions and probably of abundant moisture; it is possible that this animal may prove to be a *Megalonyx*. The mammoth (*? E. columbi*) frequented the forests of the river or lake borders. There were several varieties of horses, including especially

[1] Cope, E. D., The Silver Lake of Oregon and its Region. *Amer. Natural.*, Vol. XXIII, 1889, pp. 970–982.

[2] Shufeldt, R. W., A Study of the Fossil Avifauna of the Equus beds of the Oregon desert. *Jour. Acad. Nat. Sci. Phila.*, Vol. IX, 1892, pp. 389–425.

the types *E. pacificus* and *E. occidentalis*. The most numerous forms next to the horses were the cameloids, animals identical neither with the existing camel nor llama, referred by Cope to the genera *Eschatius* and *Camelops*, and distinguished from recent llamas (*Auchenia*) by the greater reduction of the premolar teeth, a feature which is especially marked in the genus *Eschatius*. This animal is also found in the valley of Mexico. Among the burrowing forms were the pocket gophers (*Thomomys bulbivorus*, *T. clusius*). *Geomys* also occurs. Hares (*Lepus campestris*) are very abundant. The peccaries are represented by two species of *Platygonus*. There are also prong-horn antelopes (*Antilocapra*). The only carnivore recorded by Cope is the prairie wolf, or coyote (*C. latrans*), but Matthew has added the gray wolf (*C.* cf. *occidentalis*) [1] an animal of the size of the timber wolf. The record of a bear (*Ursus*) by Cope is not confirmed. The arrowheads and flints found on the surface of these deposits are probably of recent age.

Silver Lake avifauna and climate. — It is a very fortunate circumstance that the contemporaneous bird life of Silver Lake is fully known through the rich deposits investigated by Shufeldt [2] (1892). The bird life was very abundant and not very dissimilar from what we might observe at any of the alkaline lakes of the West, resorted to at the present day by the wild fowl during their migrations. Great flocks of swans (*Cygnus paloregonus*), geese (*Anser condoni*), and ducks were there; a cormorant (*Phalacrocorax*) was among the rarities; among the species of grebe is one (*Podiceps occidentalis*) still frequenting this region. There were also coots (*Fulica minor*) and herons (*Ardea paloccidentalis*). Other forms of birds include two species of grouse, crows, and eagles. The strangest figure upon the scene among the birds was a true flamingo (*Phœnicopterus copei*). The northernmost distribution of the flamingoes at present is southern Florida and the Bahama Islands (lat. 27° N.). Shufeldt concludes that the climate might well be compared with that of Florida or the lower part of Louisiana, that the vegetation was fully as luxuriant as it now is in those parts, and that the palms were abundantly represented. This conclusion as to a Floridian climate and the existence of palms is, however, very questionable. Brown [3] observes that the South American flamingoes (*Phœnicopterus chilensis*) migrate as far south as the lakes in central eastern Tierra del Fuego, lat. 53° S., where they are said to breed, and certainly spend a part of the season. This region corresponds in temperature to the climate of central Alberta, Canada, 400 miles north of Silver Lake. Thus it appears that the presence of *Phœnicopterus copei* at Silver Lake has little weight in the determination of climate. It is more probable that the northern lakes of that period contained molluscs on which the flamingoes fed.

[1] Matthew, W. D., List of the Pleistocene Fauna from Hay Springs. *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI, Sept. 25, 1902, pp. 317–322.

[2] Shufeldt, R. W., A Study of the Fossil Avifauna of the Equus beds of the Oregon Desert. *Jour. Acad. Nat. Sci. Phila.*, Vol. IX, 1892, pp. 389–425.

[3] Mr. Barnum Brown in a note to the author.

Gilbert's [1] review (pp. 303–305) of the total fauna of the Bonneville and Lahontan basins led him to the conclusion that the life throws little light on the question of climate; in other words, it is inconclusive. He pointed out that the testimony of the freshwater molluscs, which are similar in the Bonneville, Lahontan, and Christmas Lake basins, so far as it goes, points to the conclusion that the lacustral epochs were epochs of relative cold, and favors the correlation of the high-water periods with the periods of largest glaciers.

(2.) *Late Phases of the Equus Zone*

These late phases of the Equus Zone are apparently distinguished by the absence of true camels and the presence of bison. At several points there is evidence of the existence of man in the presence of palæolithic spear or arrowheads.

The fauna is imperfectly known, and the above distinction between 'early' and 'late' is rather arbitrary at present.

Early and late Pleistocene life of Kansas. — The geologic age of the widely scattered Pleistocene deposits of Kansas still awaits determination through the careful examination and comparison of the species. Williston, Haworth, Hay, and Darton agree in a broad way on the following geologic succession:

Plains marl = loess = Pleistocene.
Mortar beds = Ogallala Formation = Pliocene + Upper Miocene.

The uppermost Miocene and Pliocene is dominantly sandy, gravelly, and clayey, the consolidation into the so-called 'mortar beds' being due to the penetration of water and presenting no test of geologic age. The plains loess, or 'marl' (Hay) is a very irregular mantle; in places it is still in process of formation as an æolian accumulation over sodded surfaces. Near the base Matthew has collected well-petrified bones of *Equus;* near the top one finds unfossilized bones of the recent bison. Some of the principal localities are as follows:

Twelve-mile Creek near Russell Springs, Logan County, Kansas (Fig. 194, 20).
'Sternberg's Elephant Bed,' Logan County, Kansas (Fig. 194, 20).
Goodland, Sherman County, Kansas (Fig. 194, 20, approximately).
Harper Township, McPherson County, Kansas (Fig. 194, 19).

McPherson County, Kansas.[2] — The watershed between the Kansas and Arkansas river systems crosses at right angles a shallow trough about ten miles wide in McPherson County. This trough contains sediments consisting of:

[1] Gilbert, G. K., Lake Bonneville. *Monogr. U.S. Geol. Surv.*, Vol. I. Washington, 1890.

[2] Lindahl, J., Description of a Skull of *Megalonyx leidyi*, n. sp. *Trans. Amer. Philos. Soc.*, n.s., Vol. XVII, Jan. 2, 1891, pp. 1–10.

4. Fine dull-orange colored loam, upward of seventy-five feet in thickness, occasionally resembling loess.
3. Stratum of volcanic dust several feet in thickness, also seen at other localities, extending twelve miles across the trough.
2. Stratum of clay, not of great horizontal extent.
1. Gravel and sand containing boulders, clay, fragments of Cretaceous shales. Remains of *Megalonyx*, *Equus*.

In the bottom of these fluviatile gravels a skull of *Megalonyx leidyi* was discovered by Lindahl, as well as remains of *Equus*. If *Megalonyx* was a

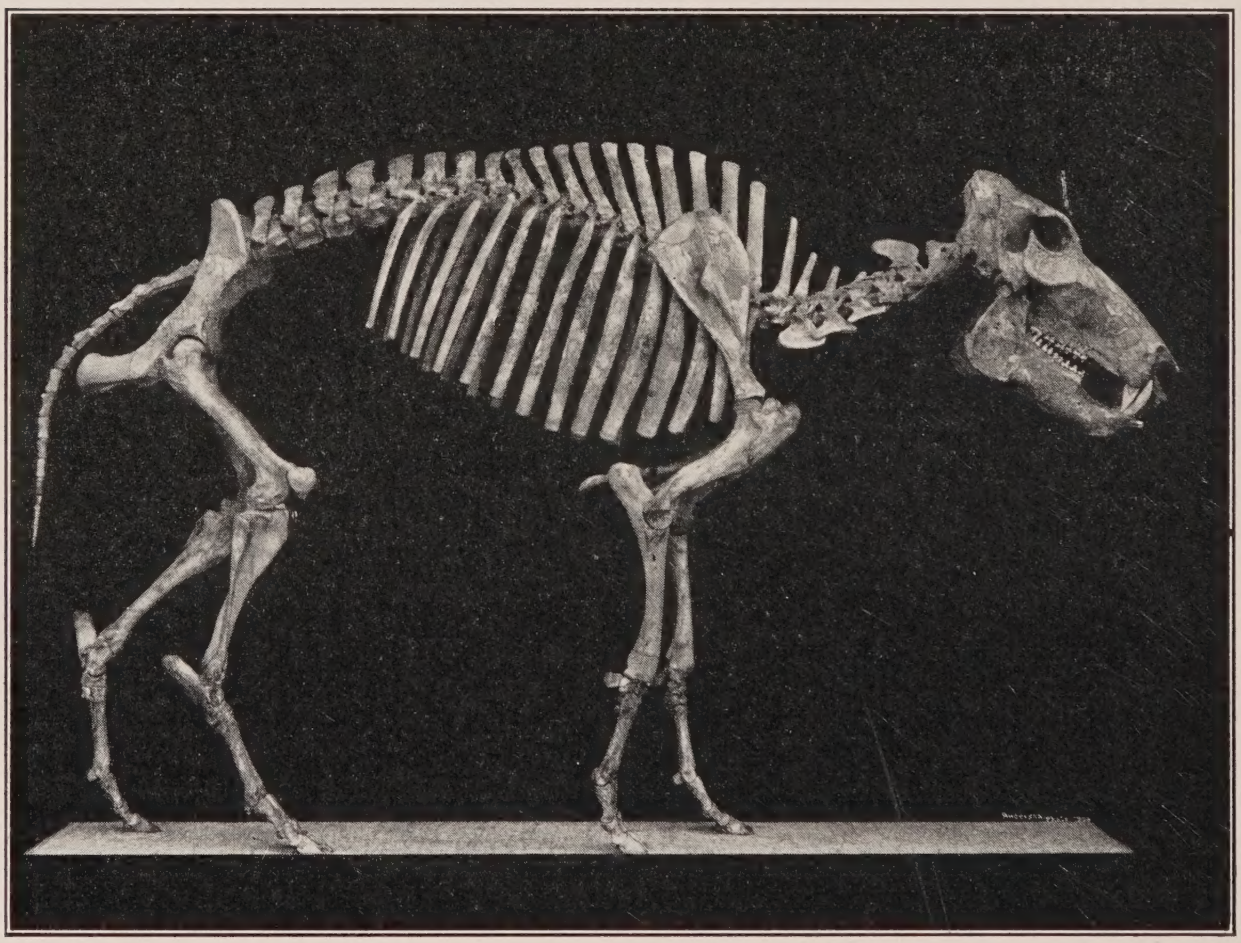


Fig. 201. — Skeleton of the Lower Pleistocene peccary *Platygonus leptorhinus*. In the American Museum of Natural History.

forest-dweller, this discovery affords some evidence that it followed the river-border forest lines into Kansas in early Pleistocene times, also that it was capable of withstanding considerable cold. The study of the region and the deposits shows that the making of the gravel and sand was coincident with a period of increasing humidity; also that ice-flooding may have been present as an effective transporting agency.

Goodland, Sherman County, Kansas. — In 1894 a most interesting discovery was recorded by Williston at Goodland, north of Fort Wallace, in the extreme western part of the state.[1] Nine specimens of the large peccary

[1] Williston, S. W., Restoration of *Platygonus*. *Kansas Univ. Quart.*, Vol. III, 1894, pp. 23–39.

Platygonus (*compressus*) *leptorhinus* were found lying close together as though a herd of the animals had been overcome by some sudden catastrophe. They lay about nine feet below the surface, with heads directed toward the southwest, the heads of the hinder lying upon the posterior parts of the more anterior ones, and the bones all or nearly all in the position they had been at the time of the animals' death. This crowding together would indicate that the animals were overtaken either by a dust storm, a snowstorm, or a blizzard, just as herds of sheep are found at the present time.

'*Sternberg's elephant bed*,' also in Logan County, Kansas, contains numerous remains of the Columbian mammoth (*E. columbi*), a large species of wolf (*Canis*), as well as a smaller canid of about the size of a coyote.

Fig. 202. — The Lower Pleistocene peccaries of North America of the genus *Platygonus*. After original by Charles R. Knight in the American Museum of Natural History.

Twelve-mile Creek, Kansas (Fig. 194, 20). — On this tributary of the Smoky Hill River has been discovered the richest deposit of the Pleistocene of Kansas. In the blue-gray layers directly underlying the recent plains layers are recorded remains of several species of mammals, including *Elephas columbi*, *Platygonus compressus*, *Bison occidentalis*. The stratum containing the bison was about two feet in thickness and composed of fine silty material of bluish-gray color. The bone bed when cleared off was about ten feet square, and contained the skeletons of five or six adult bison, of two or three younger ones, together with a fœtal skeleton within the pelvis of one of the adults.[1] The animals evidently all perished together. In

[1] Williston, S. W., On the Occurrence of an Arrow-Head with Bones of an Extinct Bison. *Trans. Internat. Congr. Americanists*, 1902, pp. 335–337.

removing the bones of the largest of these skeletons an arrowhead was discovered underneath the right scapula, imbedded in the matrix, but touching the bone itself. Williston is entirely satisfied of the authenticity of this discovery. The evidence that man was contemporaneous with the extinct species of bison (see p. 497) is of the greatest importance.

The fauna of the Kansas Pleistocene as summed up by Williston (1897)[1] was in part as follows:

Mastodon americanus
Elephas columbi
Elephas (?) imperator
Bison occidentalis
Bison alleni
Bison bison
Alces (?) sp.
Equus, several species
Platygonus compressus
Camelops kansanus
Megalonyx leidyi
Mylodon
Canis lupus
Canis (?) *latrans*
Geomys bursarius

The simultaneous death of small herds of peccaries as well as of bison points to the existence of these animals during severe conditions of climate subject either to violent winter storms, or to the prevalence of great dust clouds. A high, cold wind storm, at very low temperatures, carrying with it great volumes of dust (loess), would account for the death and rapid burial of small herds of animals seeking shelter in some gully.

2. Mid-Pleistocene Mammals of the Forested Regions. The Second Fauna

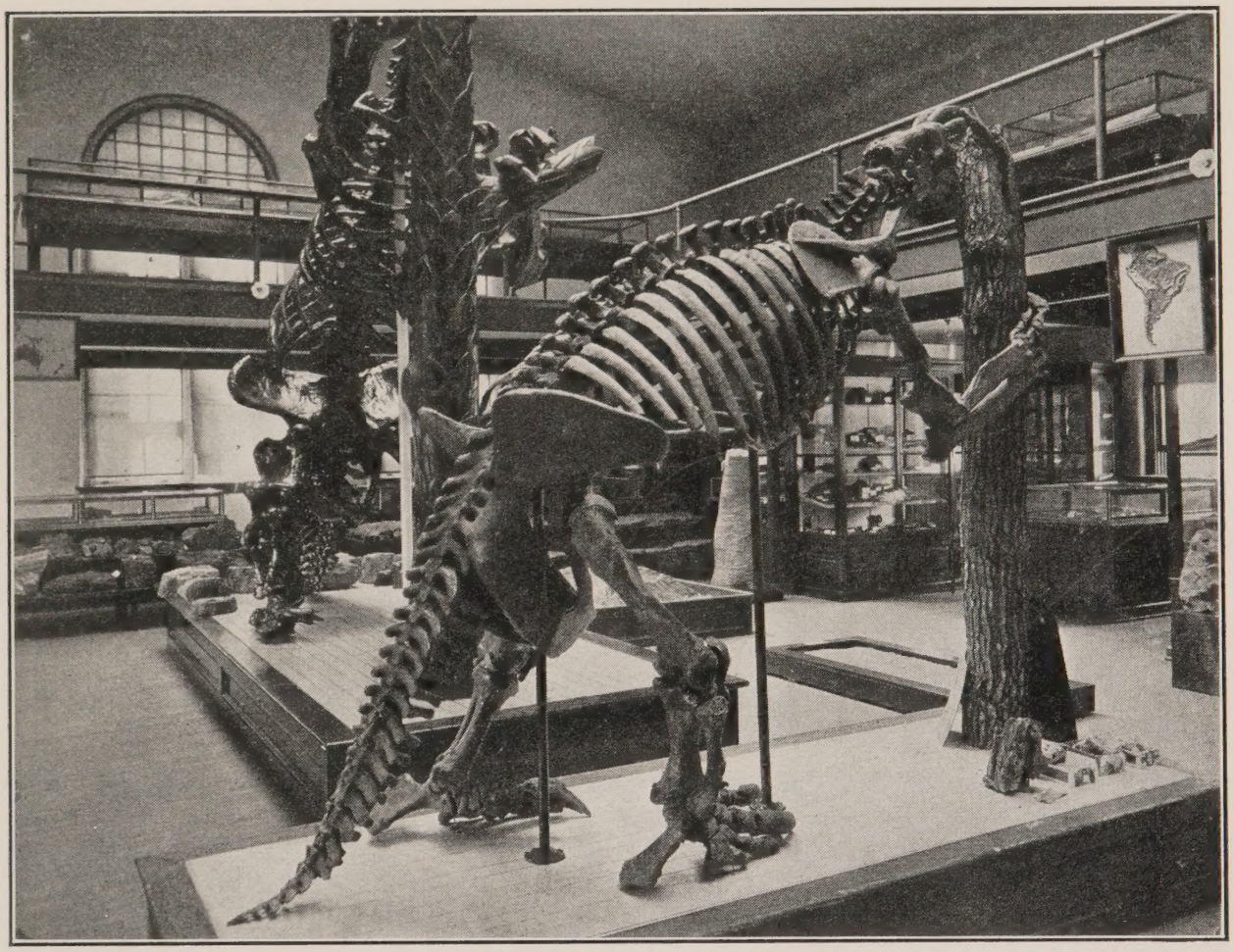
This is a temperate and south temperate, chiefly forest and meadow fauna, indicating very favorable conditions of life. Herbivorous and carnivorous mammals. This fauna is chiefly known in mid-Pleistocene times.

The second great faunal group of North America is the Megalonyx Fauna, named by Cope after the great sloth which predominated and was widely distributed from the Atlantic to the Pacific. The most important question is that discussed above (pp. 453, 454), whether this is a forest fauna contemporaneous with the distinctive plains fauna of the Equus Zone. The forest types and plains types of North America are very different to-day and were undoubtedly very different in Pleistocene times. Our present conclusion is that there are indications that the Megalonyx fauna is partly contemporaneous with, partly successive to, the plains fauna of the Equus Zone in the localities above described.

This is a rich and magnificent fauna, by no means dwarfed or impoverished. It is everywhere distinguished by the presence of *Megalonyx,* by the absence of arctic, tundra, and steppe types. It is distinctively the

[1] Williston, S. W., The Pleistocene of Kansas. *Univ. Geol. Surv. Kansas,* Vol. II, 1897, pp. 299–308.

fauna of a temperate climate, becoming north-temperate. Associated with *Megalonyx*, at least in the earlier periods of this great life zone, we find the true, or typical *Mylodon* of the East. According to the locality, whether forest, meadow, or plain, we find also the American mastodons, the Columbian mammoth, tapirs, horses, camels, peccaries, bison, and moose. The enemies of this herbivorous fauna are North and South American types of



By permission of C. S. Prosser.

FIG. 203. — The giant ground sloth, megalonyx, an immigrant from South America. Skeleton of the North American Pleistocene *Megalonyx jeffersoni*. In the Ohio State University Museum, Columbus, Ohio.

bear, very widely distributed, saber-tooth tigers, as well as large lion-like cats, and all the modern types of American canids and felids.

The American deer (*Odocoileus*) was very abundant in the forests, but it is noteworthy that the large European deer or American wapiti (*Cervus*) is nowhere recorded. We note everywhere the absence of the true musk ox (*Ovibos*), although certain of its relatives or precursors are recorded in late phases of this zone, and are actually found in certain of the same deposits, such as the Big Bone Lick, Kentucky. It is probable, however, that such mingled deposits are successive rather than contemporaneous.

Geological conditions. — Few sections are available to show the geologic conditions under which this fauna occurred. Such sections should now be taken and published from many different points.

Characteristic mammals. — In the various grand deposits of the forested regions of the East and far West in which the mammalian life is recorded, successive phases of this great period of time, which will undoubtedly be divided into sub-zones, are indicated in the very gradual extinction of the older forms and the appearance of newer forms, including modern species. In a broad way this fauna seems to correspond with the second faunal zone of Europe, *i.e.* it contains the animal life of a temperate climate; in other words, it does not embrace any mammals of the northern tundras or steppes; neither the typical musk ox (*Ovibos*), the reindeer (*Rangifer*), nor the true northern mammoth (*E. primigenius*) are within it.

In addition to what is noted above, the prevailing mammals of this fauna appear to be as follows:

Columbian mammoth (*E. columbi*), in the west and southeast.

Mastodon (*M. americanus*), very abundant in the east, rare in the west.

Horses, fairly abundant in all parts of the United States.

Tapirs, fairly abundant in the forested regions of the east and southeast, not recorded in the west.

Llamas, no longer found in the east and southeast, but surviving in the west, perhaps in Oregon, and certainly in California until near the close of this life zone.

Mylodon, sometimes associated in earlier deposits with *Megalonyx,* disappearing in the more recent deposits.

Megalonyx, surviving throughout, abundant in the east and on the Pacific slope.

Megatherium, recorded in association with this fauna at Skidaway Island in Georgia and in South Carolina.

Bison (*B. latifrons, B. antiquus*), widely distributed in the east and west.

Moose (*Alces*), appearing in the west, doubtfully recorded in the east.

Virginia deer (*Odocoileus*), abundant.

The peccary (*Mylohyus*) replaces *Platygonus,* or represents it in the forest fauna.

Relatives of the great musk sheep, or musk ox (*Euceratherium, Preptoceras*), appearing in late deposits in the west.

Mountain goat (*Oreamnos*) of the rupicaprine family, appearing in late deposits in the west.

The marmot (*Marmota*), appearing in late deposits in the west.

Tree porcupines (*Erethizon*), widely distributed throughout the United States.

Castoroïdes, a giant beaver-like rodent, widely distributed in the eastern and middle states, but apparently not extending to the south.

Saber-tooth tigers (*Smilodon*), surviving throughout.
Large lions (*Felis atrox*), in the southwest and west.
Bear, of the North American black bear type (*U. americanus*), also a giant bear allied to the South American cave bear (*Arctotherium*),[1] widely distributed throughout the United States.
Old World deer (*Cervus*), not recorded.

Some of the great deposits in which the more or less successive phases of this fauna have been discovered are placed in the accompanying column in ascending chronologic order so far as their relative age can be determined at present:

More recent 9. Big Bone Lick, Boone County, Kentucky (Fig. 194, 8).
Intermediate 8. Samwel Cave, Shasta County, California (Fig. 194, 30).
" 7. Potter Creek Cave, Shasta County, California (Fig. 194, 30).
" 6. Washtucna Lake, Franklin County, Washington (Fig. 194, 32).
" 5. Rancho La Brea, the asphalt beds of southern California (Fig. 194, 28).
" 4. Ashley River, South Carolina (Fig. 194, 11).
" 3. Frankstown Cave, Blair County, Pennsylvania (Fig. 194, 3).
Earlier 2. The Port Kennedy Cave, Schuylkill River, Pennsylvania (Fig. 194, 4).
1. Afton Junction, Iowa, belonging to the first or Aftonian Interglacial epoch (Fig. 194, 23).

Aftonian Interglacial stage. — One of the most fortunate discoveries in recent years is that of a rich deposit of mammalian remains in gravels of the Aftonian Interglacial period, which lie clearly between the drifts of the pre-Kansan and Kansan Glacial epochs.[2] These mammals apparently belonged to the early part of the *Mylodon* or *Megalonyx* life zone, and are of exceptional importance in enabling us to correlate this zone with the first Interglacial epoch in North America. The specific determinations have not yet been made positive, but there is little doubt that we have here association of sloths, camels, bison, horses, Columbian and possibly imperial mammoths, as well as mastodons. There are also foot bones of dwarf horses which resemble those of the protohippine section. An anomalous feature is the presence of a large antler which suggests that of the wapiti, or true *Cervus*. The teeth of the horses agree in size with those of *E. paci-*

[1] The name *Arctodus* (Leidy) is in a sense preoccupied by *Arctodon*, and should not be revived, because based upon an indeterminate type.

[2] Calvin, Samuel, Present Phase of the Pleistocene Problem in Iowa. *Bull. Geol. Soc. Amer.*, Vol. XX, Mar. 18, 1909, pp. 133–152.

ficus and *E. occidentalis.* Among the equine remains are hock bones, or calcanea, of exceptional size, indicating the presence of a horse of large dimensions; and there were also small, fine-limbed types of horses. The elephant teeth chiefly belong to the Columbian mammoth, presenting about twenty enamel folds in a space of ten inches. One molar approaches the true northern mammoth (*E. primigenius*) in the possession of twenty-five folds in a space of ten inches. At the opposite extreme is a tooth which exhibits folds varying from thirteen to fifteen in ten inches, which appears to indicate the presence of the imperial mammoth (*E. imperator*). (See Fig. 190.) The identifications of *E. primigenius* and *E. imperator* in this fauna, however, await final confirmation. This would be the first positive association of these species with the Megalonyx, or Mylodon fauna in early mid-Pleistocene times.

Upper Lake Lahontan beds. — The special importance of the few mammalian remains found in the Lake Lahontan deposits is that they are definitely recorded geologically. Proboscidean bones are found in the 'intermediate gravels' in the Lahontan basins (equivalent to the gravels of the inter-Bonneville epoch), also in the 'Upper Lahontan beds' (equivalent to the 'white marl' of the Bonneville). There is no doubt that the fossils were all derived from the 'upper lacustral beds' [1]; they include an elephant (*? E. columbi*), a horse, a bison, and a llama, none of which has been identified specifically. In the same 'upper lacustral clays' an obsidian spearhead was obtained (see p. 448), positively associated with proboscidean remains; there is no doubt that the mammalian remains all belong to the time of the last great rise of the lake (*op. cit.* p. 273). The presence of bison would appear to indicate that these 'upper lacustral clays' and the fauna which they contain are of more recent date than the Silver Lake Equus beds, with which they were correlated on insufficient grounds by Gilbert in his Bonneville memoir.[2]

Port Kennedy Cave of Pennsylvania is situated on the right bank of the Schuylkill River, two miles below Valley Forge, Pennsylvania (Fig. 194, 4). As studied by Cope [3] and Mercer [4] this locality has yielded sixty-four species of mammals, of which twelve are known to be still in existence and forty to be extinct; the ratio of recent to extinct forms would, however, be greatly increased by more careful comparison and more conservative determination. The animals were apparently collected here by a series of freshwater inundations, carrying with them the clay, stones, and earth of neighboring levels, and the bones of mammals separated and scattered by

[1] Russell, I. C., Geological History of Lake Lahontan, a Quaternary Lake of Northwestern Nevada. *Monogr. U.S. Geol. Surv.*, Vol. XI, 1885, p. 238.

[2] Gilbert, G. K., Lake Bonneville. *Monogr. U.S. Geol. Surv.*, Vol. I, Washington, 1890.

[3] Cope, E. D., Description of Some Vertebrate Remains from the Port Kennedy Bone Deposit. *Proc. Acad. Nat. Sci. Phila.*, Vol. XI, 1876, Pt. 2, pp. 193–267.

[4] Mercer, H. C., The Bone Cave at Port Kennedy, Pennsylvania, and its Partial Excavation in 1894, 1895, and 1896. *Jour. Acad. Nat. Sci. Phila.*, Vol. XI, Pt. 2, 1899, pp. 269–288.

decomposition. The chasm into which these remains were swept is from sixty to seventy feet deep, and twenty to thirty feet in diameter at the mouth, with descending walls sloping inward and forming a well-like hole. It is evident that the cave was not fitted for human habitation, even if man had existed in America at the time. The remains were swept in by floods and not drawn in by animals, as in the case of many of the European caves.

Fortunately a portion of the flora is preserved, consisting entirely of modern species of temperate type, such as the pin-oak (*Q. palustris*), white oak (*Q. alba*), bur-oak (*Q. macrocarpa*), the beech (*F. ferruginea*), the hazel-nut (*Corylus*), the pitch pine (*Pinus rigida*), the plum (*Prunus*), the pig nut hickory (*Carya porcina*), the shell-bark hickory (*Carya alba*), the Virginia creeper (*Ampelopsis quinquefolia*), and the thorn (*Cratægus*) (Mercer).

Pennsylvania in mid-Pleistocene times must have been a land of forests, very similar to those of the present time. The tapirs and sloths are the only indications of temperate conditions of the winter climate or of the absence of extremely low temperatures. All the other mammals are of north temperate type. The remains of the giant sloths are most abundant, following which in order of frequency come those of the rabbits, tapirs, mastodons, and peccaries. Among the larger Carnivora, the bears were more numerous than the felines, such as the saber-tooth tigers and the jaguars. The identification of species is largely based upon well-preserved remains, and has passed under the critical eye of Cope and Mercer, but probably still awaits final and precise revision. Conspicuous by their absence are the elephants and the llamas, a fact attributable to local forested conditions because both these animals were probably living in the plains region of the West or in California at this time. One ruminant (*Teleopternus orientalis*) is described by Cope as an extinct ungulate, allied either to the deer or the camels. Matthew suggests its affinity to *Ovibos*.

The fauna is distinctly divisible into forest, glade and meadow, and fluviatile types, as follows:

The Forest Fauna

The American mastodon (*M. americanus*)
The extinct tapir (*Tapirus haysii*)
The Virginia deer (*Odocoileus*)
The extinct ground sloths (*Megalonyx, Mylodon*)
The Canadian tree porcupine (*Erethizon dorsatum*)
The squirrel (*Sciurus calicinus*)
Rabbits and picas (*Lepus, Lagomys*)
Voles, shrews, moles, and bats (*Sycium, Blarina, Scalops, Vespertilio*)
Two species of fox
Martens, wolverines, skunks, weasels (*Mustela, Gulo, Mephitis, Pelycictis*)
Giant bear allied to the extinct bear of South America (*Arctotherium haplodon*)
Black bear (*Ursus americanus*)
Lynx, eyra, and (?)jaguar (*Uncia inexpectata*)

To the forest fauna should be added an extinct species of turkey (*Meleagris altus*), as well as the frogs (*Rana*) and several species of turtles allied to modern types.

River Fauna

Belonging to the fluviatile or river fauna were the following forms:

The beaver and the otter (*Castor, Lutra*).

Meadow Fauna

To the meadow fauna may be attributed one of the sloths (*Mylodon*), as well as the following forms:

An extinct bison (*Bison*)
Two or three species of horses (*E. fraternus, E. pectinatus*)
An extinct species of peccary (*Mylohyus*)
Field mice, meadow voles and jumping mice (*Hesperomys, Microtus, Zapus*)
A giant coyote, or prairie wolf (*Canis priscolatrans*)
Two species of saber-tooth tigers (*Smilodon merceri, S. gracilis*)
The American badger (*Taxidea americana*)
A ruminant (*Teleopternus*) suggestive of affinity to *Ovibos*

It will be observed that beside the camels and the elephants there are many other absentees, or non-arrivals, in this fauna. There are no European deer (*Cervus*), no moose (*Alces*), and none of the gigantic sloths known as *Megatherium*. Giant sloths of this genus are confined to the southeastern states. The bison and the bear are the most conspicuous of the newly arriving Old World mammals which appear in this fauna. Among the surviving indigenous North American forms are the saber-tooths (*Smilodon*), the tapirs, horses, and peccaries. Among the latter the modern genus *Mylohyus* replaces *Platygonus*. *Mylohyus* is a large, long-muzzled, or dolichocephalic peccary, with vestigial upper incisor teeth; it is quite distinct from *Dicotyles*. Among the animals of South American affinity are the porcupines, and the great sloths (*Megalonyx* and *Mylodon*). It is noteworthy that several modernized species of cats, one attaining the size of the jaguar (*F. uncia*), competed with the saber-tooths; also that the bear include both the typical North American and South American types. Summarizing this fauna on the basis of these determinations, there is a great predominance of extinct forms. Out of a total of thirty-six genera ten are now extinct, and out of forty-seven identified species twenty-nine are now extinct (Mercer).

Frankstown Cave, Pennsylvania. — The rich deposits in the Frankstown Cave as investigated by Holland [1] were apparently of somewhat more recent date than those of Port Kennedy. This is a large limestone cave which has yielded remains of thirty or forty species of mid-Pleistocene mammals. On the whole it strongly confirms the Port Kennedy fauna as an assemblage of highly characteristic life of the forested regions of Pennsylvania in mid-

[1] Holland, W. J., A Preliminary Account of the Pleistocene Fauna Discovered in a Cave opened at Frankstown, Pennsylvania, in April and May, 1907. *Ann. Carnegie Mus.*, Vol. IV, nos. 3 and 4, 1908.

Pleistocene times. The absence from this cave of certain forms, such as *Mylodon* and *Equus*, may be due to local causes, since it represents a more purely forest fauna than that of Port Kennedy; it may indicate also a more recent period. The giant ground sloth (*Megalonyx*) is represented, though not abundantly. Mastodon remains (*M. americanus*) are very numerous, being represented by an adult and five or six immature specimens. The presence in this cave of these infant mastodons and of various species of artiodactyls, associated with bones of a huge bear, suggest that the latter preyed upon these animals. This bear (*Arctotherium haplodon*) is a huge form related to the extinct South American bear; it was somewhat larger than the modern grizzly, and capable of attacking the young mastodons. There are a number of peccaries, one of which (*Mylohyus pennsylvanicus*) is a large animal with long tusks. Bison and three kinds of deer are found, one of the latter a large type which may represent the *Cervalces* of Scott, a moose. The small herbivorous and carnivorous fauna is similar to that of Port Kennedy. Again we note the absence of remains of the mammoth, reindeer, musk ox, and of the southerly *Megatherium*. It is a somewhat hardy temperate fauna.

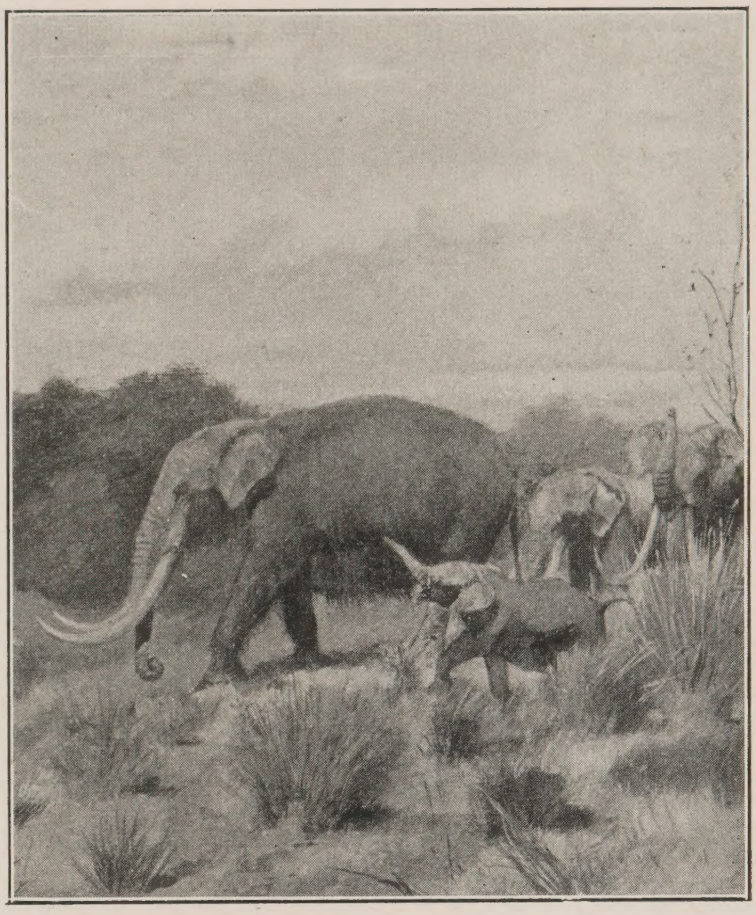


FIG. 204. — Group of American mastodons (*M. americanus*). After original by Charles R. Knight in the American Museum of Natural History.

Ashley River, South Carolina (Fig. 194, 11). — These deposits of the Ashley River Formation of South Carolina attracted the attention of Gibbes and Agassiz as early as 1845, and were seriously examined by Leidy; but we owe chiefly to Francis S. Holmes [1] the study of the geologic conditions. The principal locality is at Ashley Ferry in a bluff about thirty feet

Equus fraternus
Tapirus americanus
Mastodon americanus
Megalonyx
Bison latifrons,
species abundant in the southeast

[1] Holmes, F. S., Remarks on a Collection of Fossils from the Post-Pliocene of South Carolina. *Proc. Acad. Nat. Sci.*, July 12, 1859, pp. 177–185; *ibid.*, Remains of Domestic Animals among Post-Pliocene Fossils in South Carolina. *Amer. Jour. Sci.* (Ser. 2), Vol. XXV, 1858, pp. 442–443.

Hipparion
Megatherium
Mylodon harlani
Procyon
Didelphys
Fiber
Castor
Alces
Dicotyles

high, having at its base a Pliocene limestone composed of marine shells, while the post-Pliocene layer is a shallow river formation consisting of yellow sands with bands of ferruginous clay four feet in thickness.

The fossilized teeth are brown or black in color. The remains of ancient or extinct species of animals are mingled with those of recent species; thus the fossil tapir which occurs there, not distinguishable from the living *T. americanus*, is an animal also distributed in Texas, Louisiana, Kentucky, Mississippi, Indiana, Ohio, and South Carolina. Again, the common gray rabbit (*Lepus sylvaticus*) is associated with fragments of the teeth of the great *Megatherium* and *Mylodon*. The original specific identifications are very doubtful, and are therefore omitted in the table opposite.

The species of horse found here (*E. fraternus*) is characteristic of the southeastern United States; it represents an animal of intermediate size with teeth scarcely larger than those of the domestic donkey (*E. asinus*), and of a very complex pattern.

Rancho La Brea, southern California (Fig. 194, 28). — In southern California, about nine miles west of Los Angeles, is what promises to be the most remarkable deposit of Pleistocene mammals thus far discovered in America. As described by Merriam [1] (1906) this deposit is fifteen feet or more in thickness and a quarter of a mile in extent. It is located immediately over a sharp fold of rock, heavily impregnated with petroleum, which, issuing to the surface, has evaporated, forming springs and pools of tar which have dried and hardened locally to the consistency of asphalt. It contains scattered bones in a remarkably fresh condition, and pieces of partly lignitized wood. The remains are those of mammals and birds. Among the latter are ducks, geese, pelicans, eagles, condors, and peacocks. The smaller mammals include mice, rabbits, and squirrels; the larger are represented by extinct species of coyotes, giant wolves, bear, saber-tooth tigers, horses, bison, camels, mammoths, and large ground sloths. In the early stages of the accumulation of the asphalt, the gummy surface apparently acted as a trap for unwary animals: where there were pools of water the water birds of all kinds were entrapped in the soft tar about the margins, while the land birds and smaller mammals were ensnared in attempting to reach the water. The larger percentage of the birds are water forms, and the larger herbivorous mammals are for the most part represented by young individuals. A relatively large number of carnivorous animals corresponds with what is observed around recent asphalt pools.

In attempting to estimate the age of this fauna we first observe the

[1] Merriam, J. C., Recent Discoveries of Quaternary Mammals in Southern California. *Science*, n. s., Vol. XXIV, no. 608, Aug. 24, 1906, pp. 248–250.

association of horses, mylodont sloths, saber-tooth cats, camels, and Columbian mammoths, indicating the life of mid-Pleistocene times. With these animals also occur the bison. The absence of remains of mastodons and tapirs may be due to local causes, since this fauna is chiefly that of the open plains or meadows which surrounded this ancient asphalt lake. The chief forest types thus far mentioned are the deer and the squirrrels.

Among the characteristic species of mammals thus far recorded are two species of wolves, a saber-tooth (*Smilodon californicus*), a leonine cat (*Felis*

Fig. 205. — Rancho La Brea, California. Water pool with asphaltic margin and tar oozing out at many points. Great numbers of animals have been entrapped at such localities in the past. Recently a barn owl was caught in the tar at the edge of the pool. Photograph by J. C. Merriam, 1909.

atrox bebbi), a bison (*B. antiquus*), a mammoth (*? E. columbi*), a sloth (*Paramylodon nebrascensis*), and a horse (*E. pacificus*). Among the birds, according to the studies of Miller,[1] the raptorial species predominate. No less than thirty-three individuals of the golden eagle (*Aquila chrysaëtos*) have been recovered. Among the non-predaceous birds are the great blue heron (*Ardea herodias*), the American raven (*Corvus corax*), the Canada goose (*Branta canadensis*). A new form is *Teratornis*, a raptorial type. Especially novel is the determination of a fossil peacock,[2] because the

[1] Miller, L. H., *Teratornis*, a New Avian Genus from Rancho La Brea. *Univ. Cal. Publ., Bull. Dept. Geol.*, Vol. V, no. 21, Sept., 1909, pp. 305–317.

[2] Miller, L. H., *Pavo californicus*, a Fossil Peacock from the Quaternary Asphalt Beds of Rancho La Brea. *Univ. Cal. Publ., Bull. Dept. Geol.*, Vol. V, no. 19, 1909, pp. 285, 289, Pl. 25.

Phasianinæ belong to a group hitherto unrecorded in America. The present range of the sub-family of peacocks is now limited to the Oriental region of southern Asia, but fossil forms are recorded from the Miocene, Pliocene, and Pleistocene of Europe, and from the Siwalik beds of India. The occurrence of this species (*Pavo californicus*) in America is therefore to be con-

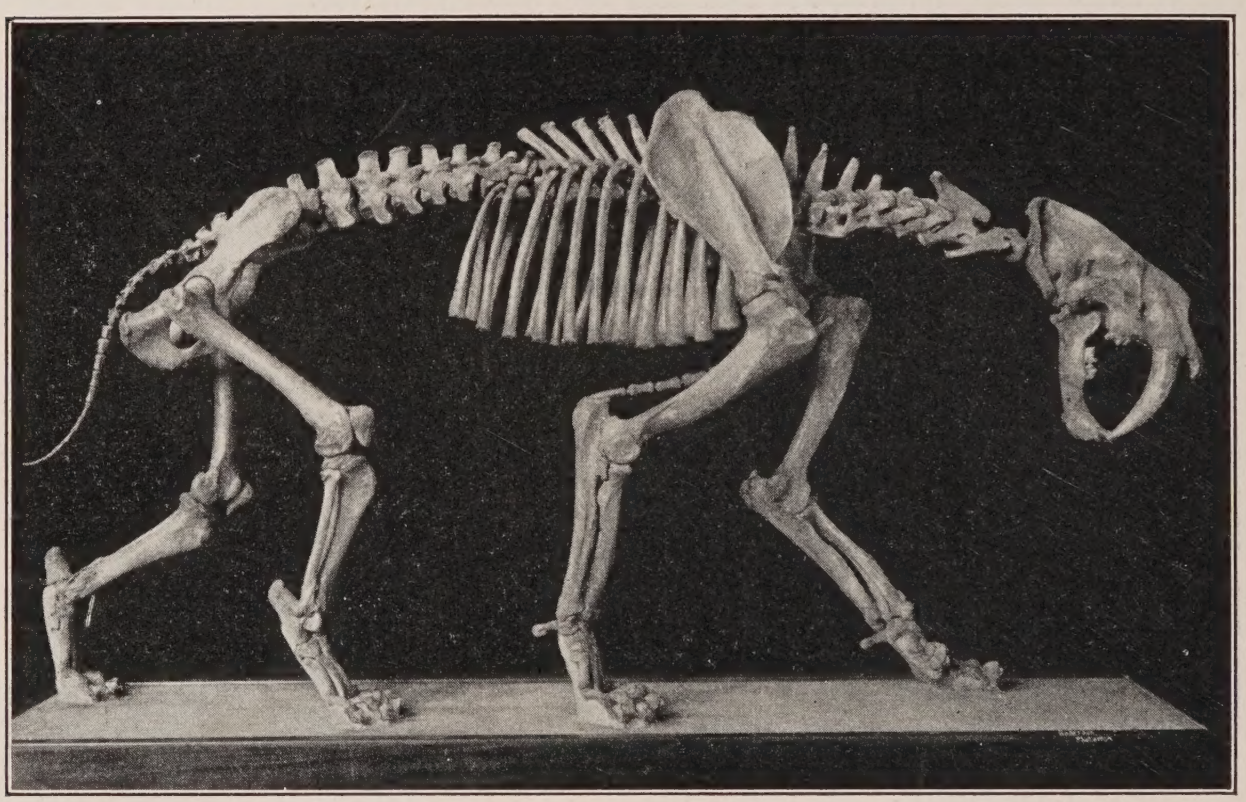


Fig. 206. — Skeleton of the great South American saber-tooth 'tiger' *Smilodon neogæus* of the Pampean Pleistocene. In the American Museum of Natural History.

sidered in connection with the Pliocene invasion (p. 337) of the Pacific Coast by Asiatic antelopes.

At *Washtucna Lake,* Franklin County, Washington[1] (Fig. 194, 32), there is a large proportion of forest and mountain types but there are no aquatic mammals.[2] Whether the animals found here are truly associated in the same level is not known. In the same neighborhood are boggy springs from which *Elephas columbi* and a species of *Bison* have been obtained, a fact which adds to the suspicion that this is a mixed fauna. This appears to belong to the latter part of the *Equus-Mylodon-Camelops* Zone, and associated with these plains-living forms are remains of distinctively forest types, including two species of moose (*Alces*) and of Virginia deer (*Odocoileus*), as well as of a mountain sheep (*Ovis montana*). Among the felids we find the puma (*Felis concolor*), and a larger leonine cat (*F. imperialis*), as well as the lynx (*F. canadensis*).

[1] Cope, E. D., The Vertebrate Fauna of the Equus Beds. *Amer. Natural.*, Vol. XXIII, 1889, pp. 160–165.

[2] Matthew, W. D., List of the Pleistocene Fauna from Hay Springs, Nebraska. *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI, Art. xxiv, Sept. 25, 1902, pp. 317–322.

Afton, Indian Territory [1] (Fig. 194, 18), is situated in the midst of a plain in the extreme northeastern part of Indian Territory, or north of the Arkansas River near its northern tributary, the Grand. In or near a spring were found one hundred mastodon teeth, twenty mammoth teeth, beside a considerable number of teeth of fossil bison and horse, as well as an entire deposit of implements and recent bones. The prevalence here of the great extinct mammals may be attributed to their frequenting the spring in wet

FIG. 207. — The Lower Pleistocene saber-tooth tiger *Smilodon neogæus*, based on a skeleton from the Pampean Formation of South America. After original by Charles R. Knight in the American Museum of Natural History.

seasons. Especially interesting is the identification of both varieties of the mammoth, the Columbian and the imperial mammoth. The human implements and remains of more recent animals are matters of secondary association (see p. 496).

The *Erie Clays* (Fig. 194, 5) are extensive deposits on the southern shores of Lake Erie, near Cleveland, constituting a 'forest bed' containing mastodon, elephant, and *Castoroïdes*.[2]

Potter Creek Cave, California[3] (Fig. 194, 30). — Environmental conditions of the Pacific coast were quite different from those in the Middle and Southern

[1] Holmes, W. H., Flint Implements and Fossil Remains from a Sulphur Spring at Afton, Indian Territory. *Ann. Rept. U.S. Nat. Mus.*, 1901, pp. 233–252.

[2] Dana, J. D., Manual of Geology. 4th edition, 1895.

[3] Sinclair, W. J., A Preliminary account of the exploration of the Potter Creek cave, Shasta County, Cal. *Science*, n.s., Vol. XVII, no. 435, May 1, 1903, pp. 708–712; Sinclair, W. J., The Exploration of the Potter Creek Cave. *Univ. Cal. Publ. Am. Arch. Ethnol.*, Vol. II, No. 1, 1904, pp. 1–27; Sinclair, W. J., New Mammalia from the Quaternary Caves of California. *Bull. Dept. Geol. Univ. Cal.*, Vol. IV, 1905, pp. 145–161; Sinclair, W. J., and Furlong, E. L., *Euceratherium*, a New Ungulate from the Quaternary Caves of California. *Bull. Dept. Geol. Univ. Cal.*, Vol. III, 1904, pp. 411–418; Merriam, J. C., Recent Cave Exploration in California. *Amer. Anthropol.*, n.s., Vol. VIII, April-June, 1906, pp. 221–228.

states. The glaciation on this coast occurred comparatively late in Pleistocene times, and was of the Alpine type, that is, confined to the higher mountain levels. It is quite possible, therefore, that many kinds of mammals, such as the elephants and camels, survived in the comparatively mild climate of the Pacific after they had become extinct in more easterly regions. These suggestions are made in the course of the admirable studies of Merriam, Sinclair, and Furlong (1903–1906) on the very rich fauna of Potter Creek Cave in Shasta County. The life here is quite as varied as that of Port Kennedy, but there are many more still existing species. Out of thirty-seven genera and forty-nine species of mammals, eight genera and twenty-two species are known to be extinct, while thirty of the genera and twenty-two of the species correspond with living forms. The now extinct forms found in this cave are the giant bear (*Arctotherium*), peccaries, camels, ground sloths, mastodons, mammoths, and the horses. This includes the entire large fauna, excepting the Virginia deer. The living forms found in this cave embrace nearly the entire existing mammalian fauna of northern California, Oregon, and Washington, with the exception of the mountain sheep (*Ovis montana*) and the wapiti (*Cervus*), neither of which occur in the Potter Creek deposits. Conspicuous among the new arrivals is the mountain goat (*Oreamnos*), the first member of the rupicaprine division of the antelope family to be recorded in North America. Here also occurs an extinct ungulate (*Euceratherium*) with affinities to the sheep (*Ovinæ*) and to *Ovibos*.

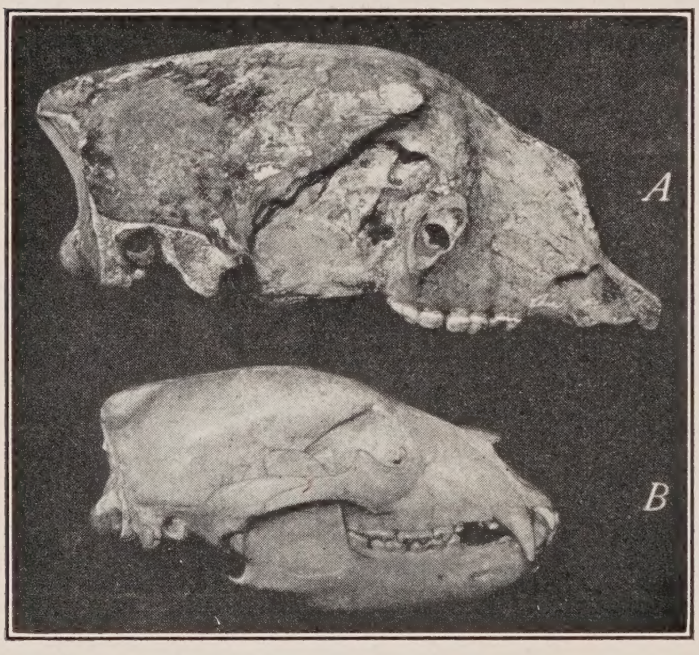


Fig. 208. — Skulls of (*A*) American extinct bear *Arctotherium*, (*B*) recent black bear *Ursus americanus*. In the American Museum of Natural History.

As compared with the Port Kennedy Cave or even with the asphaltum deposits, we observe the *absence* of certain very characteristic early Pleistocene forms, especially the saber-tooths (*Smilodon*) and the giant tapirs. It is of course possible that these absences are due to local causes. The saber-tooths certainly frequented the plains and pampas and survived into late Pleistocene times in North America (Conard Fissure). Similarly, *Mylodon*, the early Pleistocene sloth, does not occur here, while *Megalonyx*, a forest and foothill edentate, is abundant.

It is a very striking fact that the Columbian mammoth (*E. columbi*) is found here, as well as the forest-dwelling mastodon, this being the earliest record of the mastodon on the Pacific coast. Certainly to be reckoned

among the *older surviving forms* of California at this time are the horses of the characteristic species of the Pacific coast (*E. pacificus, E. occidentalis*) and a camelid. Here, too, are remains of the bison (*Bison* sp.). Among the smaller artiodactyls are the peccaries, doubtfully determined as *Platygonus*. It is a very striking fact that, while the American deer (*Odocoileus*) are abundant, there is no trace of the Old World deer (*Cervus*).

Preying upon this herbivorous fauna is a highly varied and, on the whole, very modern group of Carnivora. As in the Port Kennedy Cave, we observe among the Ursidæ remains both of the typical black bear of North America (*U. americanus*) and of the giant bear of South American affinity (*Arctotherium*). Among the cats is a very large species resembling the puma (*F. concolor*), and the lynx. Among the wolves and foxes we discover the gray fox of northern California (*Urocyon townsendi*), the red fox of the Cascade Mountains (*Vulpes cascadensis*), a large extinct species of wolf (*Canis indianensis*), also the badger, the raccoon-fox of California (*Bassariscus raptor*), also California types of skunks and weasels. The marmot (*Marmota*) is among the new arrivals. A small rodent fauna, chickarees (*Sciurus*), flying squirrels (*Sciuropterus*), the spermophiles (*Spermophilus*), the chipmunks (*Eutamias*), the hares and rabbits (*Lepus*, 4 sp.), the wood rats (*Teonoma, Neotoma*), the meadow voles (*Microtus*), the gophers (*Thomomys*), are of western mountain or Pacific type. We also discover here the first of the sewellels (*Aplodontia*), the ancestry of which has been traced in the American Oligocene (p. 229).

The fauna as a whole includes a mingling of plains and forest types, such as would be fitted to the topography of this region in Quaternary times; grazing camels, bison, horses, elephants may have inhabited the broad valley, while the deer roamed over the hillsides, and the higher peaks afforded a congenial home for the Rocky Mountain goat (*Oreamnos*). The cave seems to have remained open for a long time, receiving bones swept in from different levels by freshets in seasons of wet weather.

The fauna is not too old to preclude the idea of the contemporaneity of man. In the opinion of certain anthropologists (Putnam) the presence of *Homo* is indicated by the fashioning of bone implements; others (Merriam, 1906) regard this evidence as inconclusive (see p. 498).

Samwel Cave. (Fig. 194, 30). — In Samwel Cave, Shasta County, California, as described by Furlong,[1] has been discovered a mammalian fauna of somewhat more recent origin than the Potter Creek Cave. Split bones with polished surfaces and chipped obsidian and basalt fragments have been found here which may represent the work of man; in fact, Putnam (1905) [2] considers that man existed at this time in California. The

[1] Furlong, E. L., The Exploration of Samwel Cave. *Amer. Jour. Sci.*, Ser. 4, Vol. XXII, no. 129, Sept., 1906.

[2] Putnam, Evidence of the Work of Man on Objects from Quaternary Caves in California. *Amer. Anthrop.*, n.s. Vol. VIII, 1905, pp. 229–235.

opinions of Putnam and Merriam on this point will be cited on a later page. Of the twenty species of mammals determined here, about one quarter, or 25 per cent, are extinct. Of the characteristic animals of the mid-Pleistocene, or Megalonyx Zone, there still remain *Megalonyx*, the Columbian mammoth, and the western horse, which appear to be in this locality the last survivors of this great mid-Pleistocene fauna. No mylodonts, mastodons, or camels occur. The American black bear (*U. americanus*) is found here, but the giant South American bear (*Arctotherium*) is not recorded. Of the newcomers the sheep-like ungulate (*Euceratherium*), with affinities to the musk ox, again occurs, as well as a related form (*Preptoceras*). The remainder of the fauna is the modern characteristic mountain fauna of North America, similar to that described above at Potter Creek, and very similar to that of the present day with the exception of the fact that the wapiti, or European deer (*Cervus*), is still absent.

Big Bone Lick, Kentucky. (Fig. 194, 8). — One of the most famous of these deposits is that known as the Big Bone Lick, Kentucky, discovered in 1830, twenty miles southwest of Cincinnati, where remains of enormous herds of mastodons and Columbian mammoths are mingled with more sparse remains of other members of the Megalonyx fauna. From the very early account of Cooper [1] we take these notes. The relative frequency is a point of especial interest, as shown in the following table:

Mastodon americanus	100 individuals
Elephas columbi	20 individuals
Bison antiquus [2]	2 individuals
Bison latifrons [2]	1 individual
Odocoileus virginianus	2 individuals
Cervus canadensis	(?)individuals
Alces americanus	(?)individuals
(?)Rangifer	
Ovibos	
(?)Equus	
Megalonyx jeffersoni	

A feature of great interest is the occurrence here of *Ovibos* and *Rangifer*, two members of the *third* Pleistocene fauna. In fact, the presence of the true deer (*Cervus*), the musk ox (*Ovibos*), and the reindeer (*Rangifer*), if properly determined, is an indication either of the approach of the fauna of the *third* life zone, or that these Big Bone Lick deposits bridged over the periods of the *second* and *third* zones.

[1] Cooper, W., Smith, J. A., and De Kay, J. E., Report to the Lyceum of Natural History on a collection of fossil bones disinterred at Big Bone Lick, Kentucky, in September, 1830, and recently brought to New York. *Amer. Jour. Sci.*, Vol. XX, 1831, pp. 370–372; also, Cooper, W., Notices of Big Bone Lick. *Monthly Amer. Jour. Geol. Nat. Sci.*, I, 1831, pp. 158–174; 205–217.

[2] Authority, F. A. Lucas, The Fossil Bison of North America. *Proc. U.S. Nat. Mus.* Vol. XXI, no. 1172, 1899, pp. 755–771, Pll. lxv–lxxxiv.

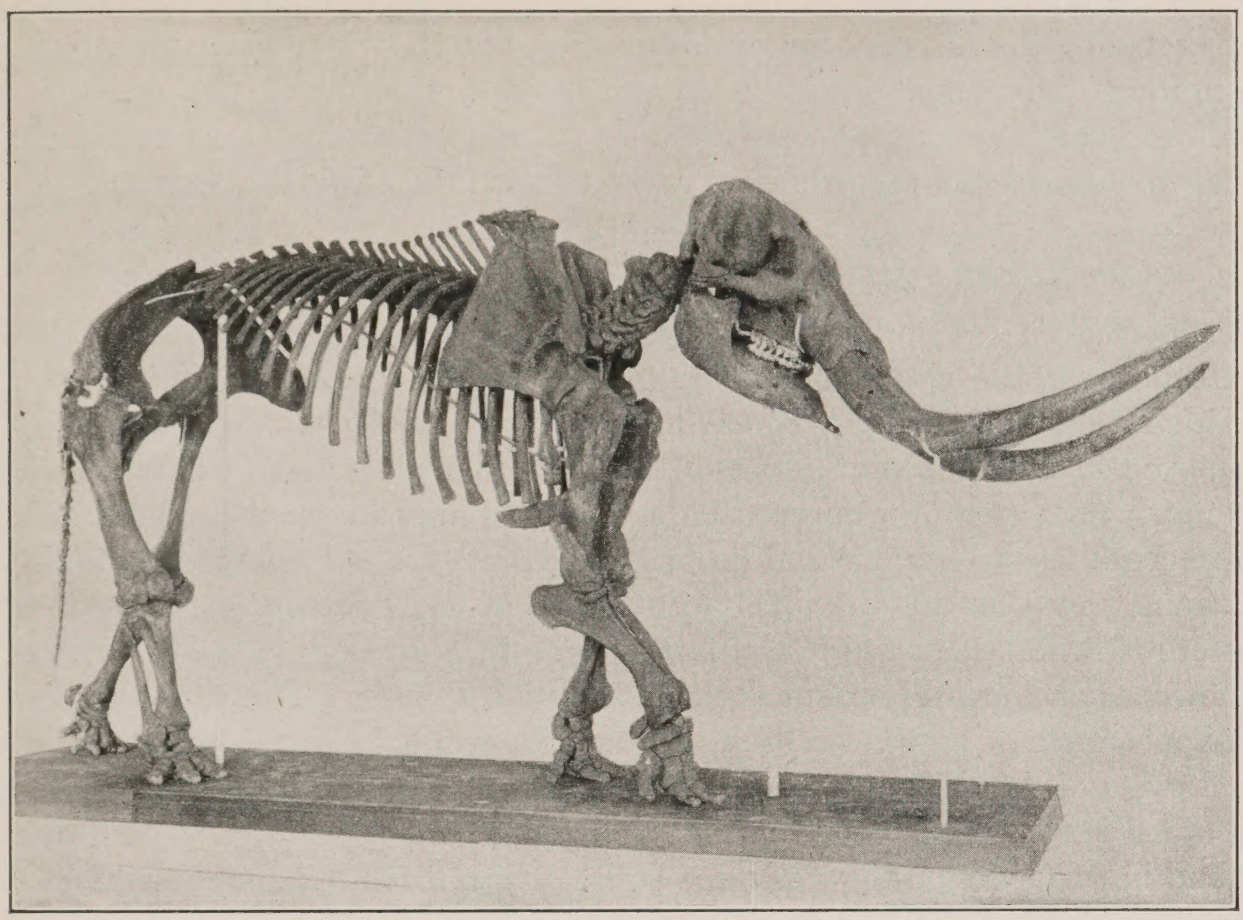


FIG. 209. — Skeleton of the famous 'Warren Mastodon' (*Mastodon americanus*), found in a Pleistocene deposit of New York State. In the American Museum of Natural History.

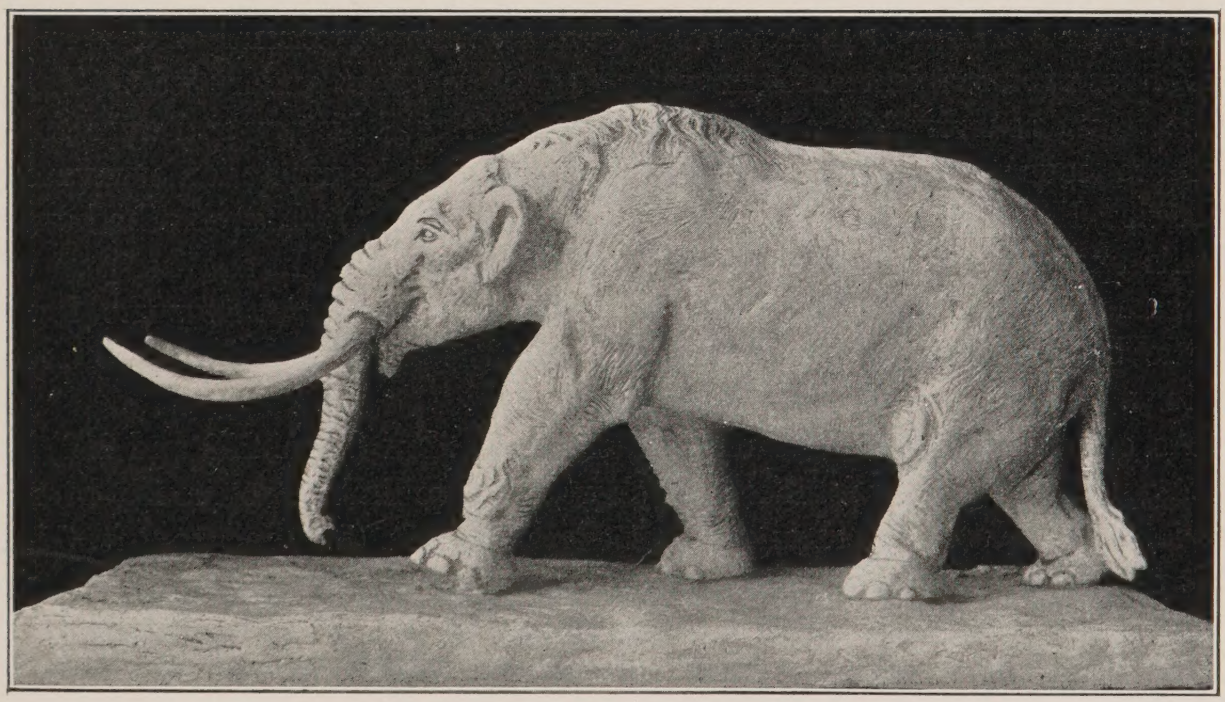


FIG. 210. — The American mastodon (*M. americanus*), modeled on the skeleton of the 'Warren Mastodon.' After original by Charles R. Knight in the American Museum of Natural History.

It would be natural to suppose that these remains were of animals attracted by the salt deposits at this locality, but the waterworn and broken condition of the bones, as well as the entire scattering of the skeletons, indicates that the remains were assembled through floods. It is remarkable that no carnivorous animals were reported with the original discovery.

Characteristic Mid-Pleistocene Mammals of the Second Fauna

Mastodons. — The known geographic range of the American mastodon extends over the entire United States northward to Lake Winnipeg and British Columbia, with a single find reported in Alaska and two finds reported in Nova Scotia. East of the Hudson and of Lake Champlain it is rare; thus very few specimens have been found in New England. In New York the geographic and geologic distribution has been most carefully examined by Clarke;[1] he finds no evidence of the existence of mastodons before the Glacial period; they first appear in New York State in what is known as the pre-Wisconsin Interglacial (see p. 444). The time of their disappearance or extinction seems to have been nearly coincident with the melting and recession of the ice floes, glacial lakes, and glacial streams, in other words, post-Glacial times. Mastodon and *E. columbi* remains are found in surface deposits above the latest glacial drift in Indiana and Ohio, and according to the opinion of some observers (Brown) these genera existed in the Central States long after glacial influence. In the western part of New York the remains are found imbedded in old glacial lake terraces caused by the damming back of ice floes. In eastern and southern New York remains are invariably found in more or less completely drained swamps and peat bogs, separated by narrow rocky divides, which apparently formed the chief lines of north and south migration of these great quadrupeds. That these animals survived to a late stage in post-Glacial history and were contemporaneous with man is especially indicated by the mastodon excavated at Attica, New York, by Clarke in 1887 (*op. cit.*, p. 864); beneath the bones of this skeleton were found several pieces of charcoal. In another part of the same swamp, under four feet of muck and one foot below the level of the bones, was found a considerable quantity of charcoal with broken pottery.

As compared with the mammoth, the mastodon (Figs. 209 and 210) is distinguished by its low forehead, its short, massive limbs, enormously broad pelvis, the height at the shoulders not exceeding 9 ft. (2.70 m.) to 9 ft. 6 in. It is probable that it was clothed with hair, with an undercoating of wool. In the only instance in which hair has been discovered it is described as coarse, long, and brown. The greatest length attained by the tusks is ten feet, the average in full-grown specimens being seven to eight feet. The

[1] Clarke, J. M., Mastodons of New York. *N. Y. State Mus., Bull.* 69, *Palæontol.* 9, Nov., 1903, pp. 921–933. See also Lucas, Animals before Man in North America, New York, 1902.

annular structure of the dentine appears to indicate (Osborn, 1908) that the growth was intermittent; an animal with tusks eight feet in length exhibits twenty-four of these growth rings, which may be interpreted as proving that it attained an age of more than twenty-four years. The indications are that mastodons were extraordinarily abundant; it is estimated by Clarke that they may have been at one time as numerous as the bison. At

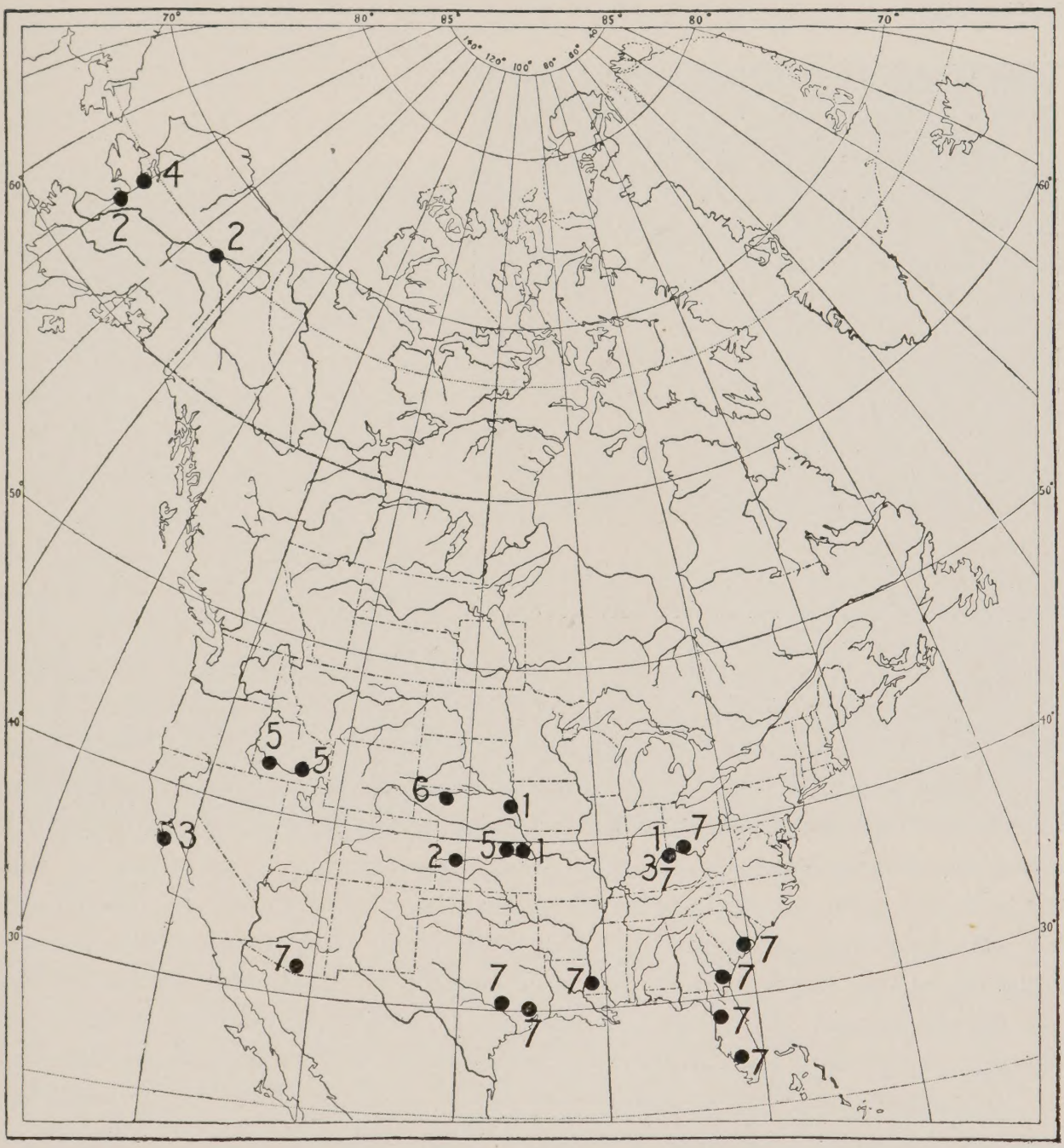


FIG. 211. — The Bison in Pleistocene times. Localities from which principal types and other specimens of fossil bison have been recorded. Authority of F. A. Lucas. **1**. *Bison bison.* **2**. *Bison occidentalis.* **3** *Bison antiquus.* **4**. *Bison crassicornis.* **5**. *Bison alleni.* **6**. *Bison ferox.* **7**. *Bison latifrons.*

Big Bone Lick, Kentucky, remains of mastodons far outnumber those of the Columbian mammoth, being five times as numerous as those of the mammoth and a hundred times as numerous as those of the bison. If these animals were contemporaneous with man in post-Glacial times, it is possible that they may have been hunted or driven to extinction through his agency.

Bison. — We owe to Allen (1876),[1] Lucas (1899),[2] and McClung (1908) [3] our knowledge of the skull and skeleton of the many kinds of great bison, or buffalo, which roamed over all parts of North America during Pleistocene times. As revised by Lucas, there are seven valid species of fossil bison, which had a widely extended geographical distribution from Florida to Alaska (Fig. 211). They also undoubtedly in part succeeded each other in geological time, the latest bisons culminating in the recent species, *Bison bison*, more or less fossilized remains of which have been discovered in Kentucky, Kansas, and in the loess deposits of Missouri.

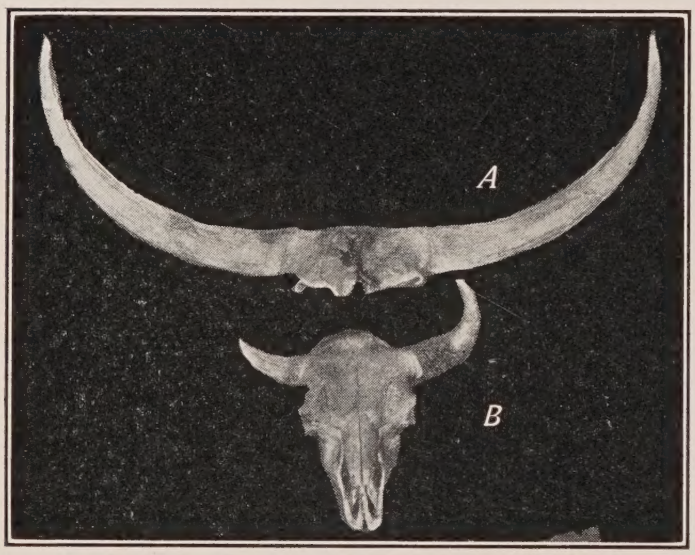


FIG. 212. — Skulls of (*A*) the extinct bison of Kansas, *B. latifrons*, and of (*B*) the recent bison of the Great Plains, *B. bison*. In the American Museum of Natural History.

The early and gigantic form (*B. latifrons*) reflects the favorable conditions of life during the Megalonyx Zone. In Texas, Mississippi, Georgia, Ohio, Kentucky, and Kansas remains of this species have been found. In some of these localities they are associated with bones of the American mastodon, the Columbian mammoth, and of the great sloths *Megalonyx* and *Mylodon*. The horn cores are so long and thick that they exceed by two feet on each side those of the existing Old and New World bison, as shown in the accompanying figure. Horns in the collection of the Cincinnati Natural History Society measure 6 ft. 6 in. (1.95 m.) along the curve from tip to tip. This measurement is exceeded by the magnificent horn cores discovered in Kansas and secured by Sternberg for the American Museum of Natural History; they measure 6 ft. across from tip to tip, and 8 ft. 6 in. (2.55 m.) along the curve; this appears to be the record in size. Although the skeleton is unknown, we may judge from the size of the skull that *B. latifrons* far exceeded any of its living relatives.

Remains of another ancient form, *Bison antiquus*, have been found in Kentucky and in California associated with remains of elephants, mastodons, horses, and camels. Although a much smaller animal, it appears to have been a contemporary of *B. latifrons* in the Megalonyx life zone, but may have survived to a more recent date. It is considerably larger than

[1] Allen, J. A., The American Bisons, Living and Extinct. *Mem. Mus. Comp. Zoöl. Harvard Coll.*, Cambridge, Vol. IV, no. 10, 1876.

[2] Lucas, F. A., The Fossil Bison of North America. *Proc. U.S. Nat. Mus.*, Vol. XXI, no. 1172, 1899, pp. 755–771.

[3] McClung, C. F., Restoration of the Skeleton of *Bison occidentalis*. *Kansas Univ. Sci. Bull.*, Vol. IV, no. 10, Sept., 1908, pp. 249–254.

B. bison, and is readily distinguished by the position of the horns, which are placed almost at right angles to the long axis of the skull. The horns of another species (*B. ferox*), resembling those of *B. latifrons*, have been found in the Pleistocene of Nebraska. The Pleistocene of Idaho and Kansas has yielded the horn cores of a fifth species (*B. alleni*). The giant northwestern bison found in Alaska, which may have existed also in eastern Siberia, is *B. crassicornis*. There also lived in Alaska, probably in late Pleistocene times, and ranged down into Kansas, the species *B. occidentalis*. This animal most closely resembled the living bison, with which it was probably contemporaneous for a time. A complete specimen of a bull of this species was

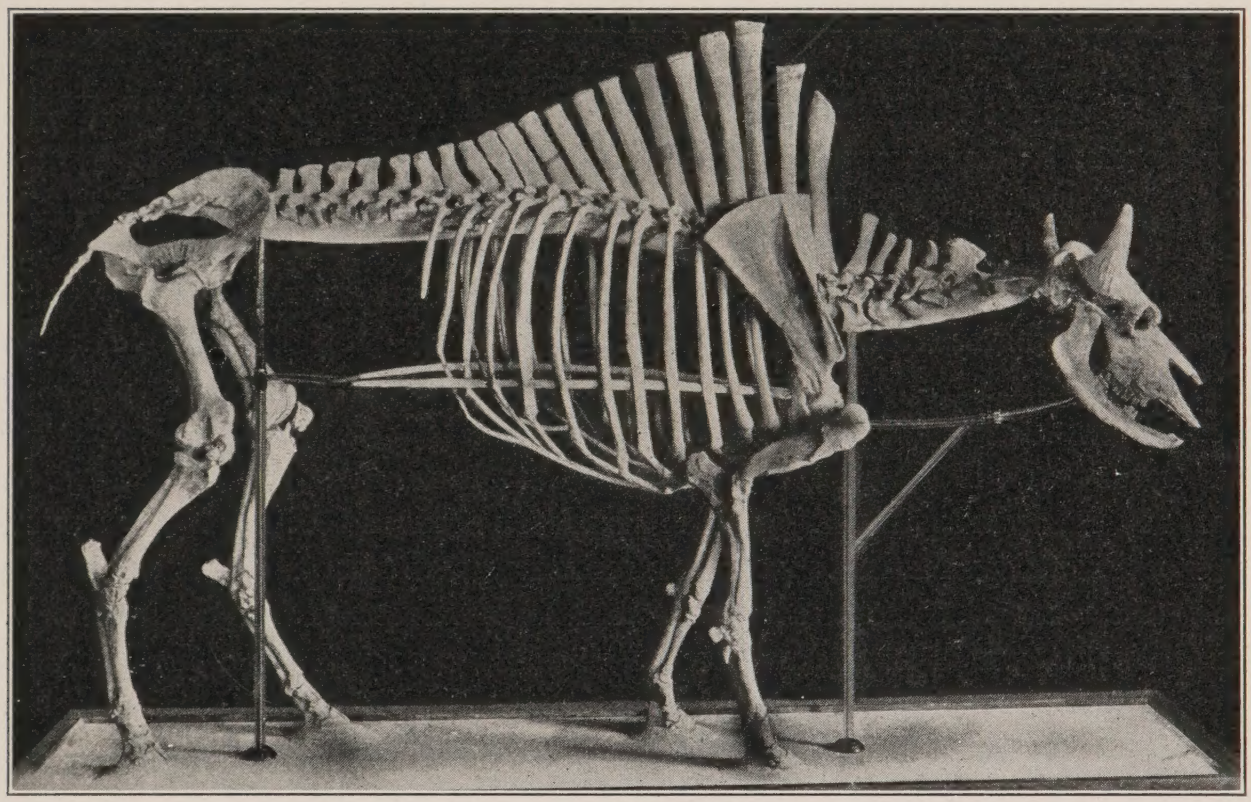


Fig. 213. — Skeleton of the extinct bison *B. occidentalis*. In the University of Kansas. After McClung.

discovered with seven or eight other skeletons near Russell Springs, Logan County, Kansas, in association with a flint arrowhead.[1] The skeleton as mounted in the Kansas Museum (Fig. 213) is considerably larger than that of the largest recent bison in length and height, and in the length of the hind limbs. The horn cores are similar in shape and proportions.

Mountain antelopes. — A late arrival in the western mountain region only is the so-called 'Rocky Mountain Goat' (*Oreamnos*). This animal is the sole representative in North America of the very aberrant group of mountain antelopes known as the chamois sub-family, or *Rupicaprinæ*, a subdivision of the Bovidæ, comprising five widely scattered animals, which are distributed on mountain heights from the Pyrenees of Spain to the

[1] McClung, Restoration of the Skeleton of *Bison occidentalis*. *Kansas Univ. Sci. Bull.*, Vol. IV, no. 10, Sept., 1908, pp. 249–254.

Rocky Mountains. These are the typical chamois (*Rupicapra*), the goral, the takin, the serow, and finally the American misnamed 'goat.'[1]

Tapirs. — The tapir of the Megalonyx Zone (*T. haysii*) has been discovered in Kentucky, Indiana, Mississippi, and South Carolina. This species is apparently more robust than the existing South American tapir. A somewhat smaller animal, referred by Leidy to *T. Americanus*, is indistinguishable in size and form from the living *T. terrestris* of Central and South America. Its remains have been found in Texas, Louisiana, Mississippi, South Carolina, Virginia, Ohio, Illinois, and California. The tapir was undoubtedly one of the most characteristic animals of the Megalonyx life zone, especially in the forests of eastern North America. It apparently migrated to the South during the period of the Ovibos life zone.

Horses. — As studied by Gidley[2] there were at least ten forms or species of horses in different parts of the United States and Mexico in Pleistocene times, distinguished by geographic distribution, by size, and by the proportions of the body and skull, and by the characters of the upper grinding teeth. The *E. fraternus*, found in the Ashley River, South Carolina, and characteristic of the southern United States, is still imperfectly known; it represents a very small horse, with teeth scarcely as large as those of the Mexican donkey and of a very complex pattern. The *E. complicatus*, first found near Natchez, Mississippi, belonging in the western, southern, and middle-western states, is a well-known animal characterized by teeth as large as those of the ordinary horse, but with a skeleton of intermediate size; the skull is especially distinguished by its short muzzle, in which respect it resembles that of an ass. From the Rock Creek Beds of western Texas comes the *E. semiplicatus*, which in certain cranial characters, as well as in the size and proportions of its teeth, seems to present a close relationship to the ass (*E. asinus*). On the Staked Plains of central Texas has been found *E. scotti* (see Fig. 14), intermediate in size between *E. complicatus* and *E. pacificus*, with a long face, relatively large head, long body, short neck, resembling in its proportions the quagga (*E. burchelli*). From southwestern Texas comes also *E. giganteus*, the largest species of horse hitherto recorded, the teeth exceeding those of the largest modern draught horses by more than one third of the diameter of the latter. In contrast with this is the *E. tau* in the valley of Mexico, the smallest true horse known in America, more diminutive than any European species living or extinct. Associated with this in the valley of Mexico is *E. conversidens*.

The type of horse found in the Middle Pleistocene forested region of eastern Pennsylvania is *E. pectinatus*, from the Port Kennedy Cave. On the Pacific slope, California, has been found *E. occidentalis*, with teeth of

[1] Grant, Madison, The Rocky Mountain Goat. *N. Y. Zoöl. Soc. New York, 9th Ann. Rept.*, 1904, pp. 230–261.

[2] Gidley, J. W., Tooth Characters and Revision of the North American Species of the Genus *Equus*. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIV, Art. ix, May 31, 1901, pp. 91–141.

uniformly simple pattern, a horse of about the size of *E. complicatus*, *i.e.* about 14½ hands. Another horse found in California is *E. pacificus*, best known, however, in Oregon; next to *E. giganteus* this is the largest American Pleistocene horse; the skeleton indicates a horse of about the size of an ordinary draught horse; the skull is proportionately larger.

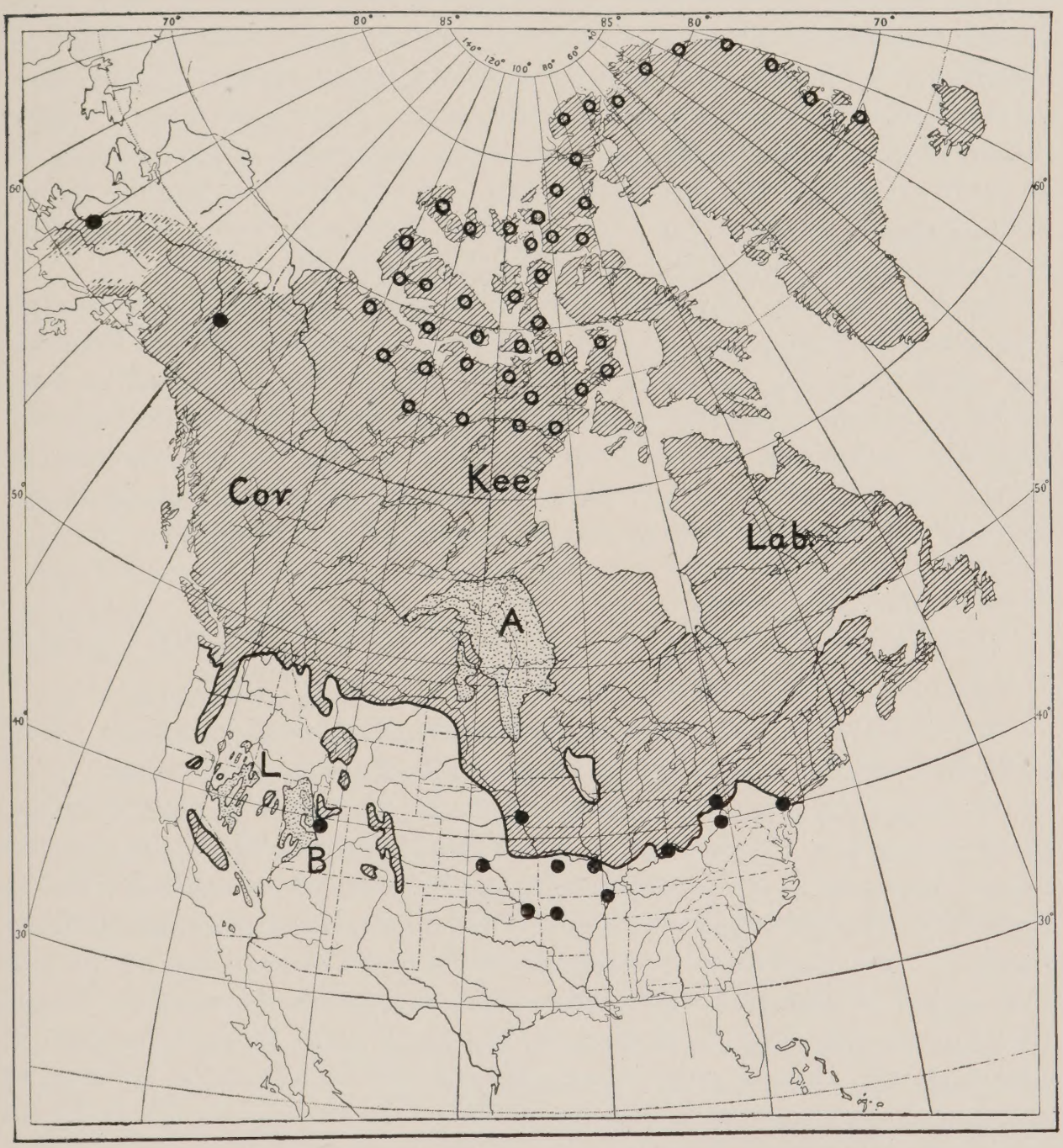


FIG. 214. — The Musk Ox in glacial and recent times. Localities in which Pleistocene fossil musk oxen have been recorded = solid black. Present distribution of musk oxen = circles. Maximum glaciation of North America shown in oblique lines. Cor = Cordilleran ice sheet, Kee = Keewacin, Lab = Labradorean. Pleistocene lakes = dotted areas. A, Lake Agassiz, L, Lake Lahontan, B, Lake Bonneville.

Lions. — It is a most interesting case of faunal parallelism that the mid-Pleistocene of America, like that of Europe, developed a leonine species of cat. This was contemporaneous with the Megalonyx fauna. Its remains were first found by Leidy in 1853 near Natchez, Mississippi, and described

as *Felis atrox*, while a larger Pleistocene form in California was named *F. imperialis*. Confirmation of its character has recently been obtained [1] in the Asphalt Beds of Rancho La Brea. The skull (*Felis atrox bebbi*) is remarkably similar to that of the existing African lion and the cave lion of the European Pleistocene. This California variety approaches closely in measurements Leidy's type jaw from Natchez, Mississippi, with some specific variations. The muzzle is very wide compared with the length of the skull. As in the European form, the superior outlines of the skull approach the lion more closely than the tiger. The related form, *F. imperialis*, from Livermore Valley, California, associated with remains of *B. latifrons*, and of *Elephas*, *Equus*, and *Canis indianensis*, possibly occurs in the Potter Creek Cave [2] and is reported at Washtucna Lake, Washington. It is undetermined whether it is really a distinct species.

Summary.— The mammals which have been described above as contemporaneous with *Megalonyx* in such widely scattered regions as Pennsylvania and California appear to constitute a great group adapted to temperate and north temperate conditions of climate. Except in the probably successive deposition of Big Bone Lick, not a single boreal, tundra, or steppe species occurs among them; on the other hand, there is a large element of hardy species of southern affinity, such as the sloths.

3. The Fauna of the Ovibos Zone, Perhaps Corresponding with the Arctic and Tundra Period in Europe

This is an impoverished fauna, reduced in numbers and in variety. Full of modern or existing species, far to the south of their present range.

We thus enter a new faunal zone, which may be called the zone of *Ovibos*, or the musk ox. The advent of this northern form in the central United States, as shown in the accompanying figure, is perhaps coincident with the period of the last great glacial advance which is recorded in the great terminal moraine. The glaciated, or partly glaciated areas of the United States at this period of maximum advance are here mapped as recorded by Dana. The known southerly distribution of the musk ox in Pleistocene times is independently plotted from various records, yet it appears to coincide in the most remarkable way with the southerly boundaries of the great ice sheet. (See Fig. 214.) The mammals of this period of maximum glaciation and of the subsequent recession of the ice may be considered together as constituting the third great life zone of the American Pleistocene, which may correspond with the third life zone in Europe.

It by no means rests upon the same positive or cumulative evidence as

[1] Merriam, J. C., The Skull and Dentition of an Extinct Cat Closely Allied to *Felis atrox* Leidy. *Univ. Cal. Publ., Bull. Dept. Geol.*, Vol. V, no. 20, Aug., 1909, pp. 291–304.

[2] Bovard, J. F., Notes on Quaternary Felidæ from California. *Univ. Cal., Publ., Bull. Dept. Geol.*, Vol. V, no. 20, Sept., 1907, pp. 155–166.

the second, or Megalonyx life zone, and cannot be described with equal certainty because only a single, rich faunal assemblage is known, namely, that of the Conard Fissure in Arkansas.

It appears to be defined negatively by the absence of great sloths (*Mylodon* and *Megalonyx*) and of the tapirs. There is less certainty as to the absence or extinction of the llamas at this time. Positively, it is distinguished by the arrival of the musk ox (*Ovibos*), the reindeer (*Rangifer*), and the Old World deer or wapiti (*Cervus*). It is important to note that in Big Bone Lick (p. 478) these disappearing and newly arriving forms are recorded together, although they may have been successively deposited. The chief localities are:

4. Alaska, 'ground ice,' Kowak clays, etc., scattered deposits.
3. Conard Fissure, Newton County, Arkansas. (Fig. 194, 17.)
2. Scattered deposits in the Middle and Western states.
1. Big Bone Lick, Kentucky, in part (see p. 487).

If the Conard Fissure of Arkansas is rightly placed in this zone, it appears that the horses still survive, although in diminished numbers. The saber-tooth tigers also survive in modified form. It is probable, but by no means certain, that the modern mammoth (*E. primigenius*) reached its most southerly distribution near the city of Washington at this time. The American mastodons certainly survived in the eastern forests. The characteristic types of this period may, therefore, be summarized as follows:

Musk oxen (*Symbos, Ovibos*), ranging south to the central states.
Reindeer or caribou (*Rangifer*).
Old World or wapiti deer (*Cervus*), in the central and southern states.
Bisons (*? B. occidentalis, ? B. bison*).
Mastodons, in the eastern forests.
Northern mammoths (*Elephas primigenius*).
Last saber-tooth tigers (*Smilodontopsis*), in the southern states.
Last horses, in the southern states.
Walrus (*Odobœnus*), along the south Atlantic coast.

Conard Fissure of Arkansas (Fig. 194, 17). — It is important to note (Fig. 214) that this locality lies about one hundred and fifty miles south of the most southerly extension of the great terminal moraine. As recorded by Brown [1] (1908) of the American Museum of Natural History, this fissure has yielded remains of thirty-seven genera and fifty-one species of mammals, of which only four genera and twenty-four species are now extinct; it thus presents a great contrast to the Port Kennedy assemblage. The presence of an extinct genus of musk ox (*Symbos*), of the wapiti (*C. canadensis*), and of many small rodents and carnivores which at the present time range far

[1] Brown, Barnum, The Conard Fissure, a Pleistocene Bone Deposit in Northern Arkansas: with Descriptions of Two New Genera and Twenty new Species of Mammals. *Mem. Amer. Mus. Nat. Hist.*, Vol. IX, Pt. iv, Feb., 1908.

north of Arkansas, shows that the climate was of a northerly type similar to that of the forested regions of British Columbia. With the exception of the musk ox — which, it must be remembered, formerly had a more southerly range than at present — it is certainly in no sense a tundra or arctic fauna. The assemblage, nevertheless, indicates the crowding southward of northerly forms, such as may have occurred during the advance of the great ice sheet. There is no evidence of the existence here at this time of *Megalonyx*, or *Mylodon*, of the tapir, mammoth, or mastodon. It would not be safe, however, to assume from this evidence that the tapir, mammoth, and mastodon were extinct in all other parts of the American continent at the time. The only four now extinct genera which give an ancient character to this fauna are the saber-tooth tiger, above mentioned, an extinct species of horse (*E. scotti ?*), an extinct genus and species of peccary (*Mylohyus*), and the extinct genus of skunk (*Brachyprotoma*), three species of which are found in the Port Kennedy Cave.

The condition of the bones and the association and predominance of certain forms indicate that this fissure was the home of several contemporaneous species which preyed on still others and brought their remains into it. Cats and bears probably inhabited parts of this cavern, dragging in peccaries and deer; weasels occupied runways in the rock, which are filled with remains of mice, rabbits, and wood rats. Shrew and mice bones were probably introduced largely by owls, which may have lived on the ledges of the fissure. The fauna is typically that of a forest region, with open glades, similar to the present conditions of the same region in Arkansas. There are five species of shrews, three of which are now extinct, a mole, two bats, one living and three extinct species of skunk. Other mustelines are the fisher marten (*Mustela pennanti*), the mink (*Putorius vison*), and the weasel. The gray wolf (*C. occidentalis*) was accompanied by the red fox (*Vulpes fulvus ?*), and the gray fox (*Urocyon* sp.). The raccoon (*Procyon lotor*) was abundant. We observe the black bear (*U. americanus*), but, as in the Samwel Cave of California, there is no evidence of the giant South American bear which is found in all the earlier Pleistocene deposits of the Megalonyx Zone. Among the cats are lynxes and pumas, beside two species of the extinct saber-tooth (*Smilodontopsis troglodytes, S. conardi*).

Among the larger Herbivora both the mule deer (*Odocoileus hemionus*) and the white-tailed deer (*O. virginianus*) are recorded, as well as the wapiti (*C. canadensis*) and the extinct genus and species of musk ox (*Symbos australis*). It is noteworthy that the peccary is not of the existing southwestern type (*Dicotyles torquatus*), but belongs to the genus (*Mylohyus*) characteristic of the Megalonyx Zone.

The small rodent fauna is that of the present forested regions of the Rocky Mountain area.

Canadian deposits. — The *Iroquois Beach* deposits (Fig. 194, 2) are considered by Canadian geologists of post-Glacial age. They contain numerous

horns of reindeer (*R. caribou*), of the mammoth (*E. primigenius*), of the mastodon (*M. americanus*), of the wapiti (*C. canadensis*), and of the beaver (*Castor fiber*).[1] Seventy feet above the lake (Lake Ontario), on Burlington Bay, the western part of the lake, has been recorded the mammoth (*Elephas jacksoni*), a type probably referable to the true mammoth.

The Alaskan fauna. — Alaska was free from glaciers except in its central mountainous belt. It presents a rich life in Pleistocene times. The bones

FIG. 215. — Map of Alaska showing localities where Pleistocene mammalian fossils have been discovered. After Dall and others. Quackenbush, American Museum Expedition, 1908.

of mammals are found widely distributed;[2] their scattered remains occur throughout the unglaciated region of Alaska and adjacent Canadian territory in several quite distinct deposits: first, in the black muck accumulated

[1] Geology of Canada, 1863, p. 914.

[2] Dall, W. H., and Harris, G. D., Correlation Papers. The Neocene of North America *U.S. Geol. Surv.*, Bull. No. 84, 1892.

in gulches and valleys of the smaller streams; second, in the fine elevated clays of the 'Yukon silts' and 'Kowak clays'; and third, in the more recent fluvial and alluvial deposits.[1] Of these the most remarkable is the 'ground ice' formation of Dall, in which solid beds of ice of considerable thickness take the place of rock strata, and are covered by beds of blue clay containing numerous remains of Pleistocene mammals. The distribution of these ground ice formations and of the 'Kowak Clays' is plotted on the accompanying Alaskan map, which combines the results of Dall and of Quackenbush, the symbols indicating our present knowledge of the distribution of the principal types of mammals. This distribution includes, beside the above, bones recorded in river gravel deposits. In some of the clays the parts preserved are so complete as to indicate that the animals were mired entire, one such specimen with portions of the hair and wool having been discovered by Quackenbush.[2]

Elephas primigenius, the hairy or northern mammoth.
Elephas columbi (determination somewhat uncertain).
Mastodon americanus.
Ovis (determination somewhat uncertain).
Ovibos moschatus, the true musk ox.
Ovibos yukonensis, an extinct species.
Symbos tyrelli, with much smaller horns than *Ovibos*.
Ovis montanus, the mountain sheep.
Oreamnos, the mountain goat.
Rangifer sp. ind., caribou, probably the 'barren ground' variety.
Bison crassicornis, a long-horned species.
Bison occidentalis, resembling the recent bison.
Bison alleni, with long, slender, much curved horns.
Alces, the moose (*? Alces americanus*).
Equus, species indeterminate.
Ursus, of the size of *U. americanus*.
Canis.
Castor, the beaver.
Odobœnus, the walrus.

Judging from the number of separate bones collected or examined by Quackenbush, the mammoth was everywhere the most abundant animal, the bison followed closely, the horse and caribou existed in lesser numbers, and other mammals were comparatively scarce. That the country was forested and the climate somewhat milder than that of the present time seems to be proven by the fact that large trees have been found associated

[1] Gilmore, C. W., Smithsonian Exploration in Alaska in Search of Pleistocene Fossil Vertebrates. *Smiths. Miscel. Coll.*, part of Vol. LI, Washington, 1908.

[2] Quackenbush, L. S., Notes on Alaskan Mammoth Expeditions of 1907 and 1908. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVI, Art. ix, Mar. 24, 1909, pp. 87–130.

with horse and mammoth remains in regions which are now barren tundras with frozen subsoil. The preservation of the flesh and hair of the mammoth found at Elephant Point was not due originally to freezing, but to burial in soft mud which protected the parts from bacterial decay; the parts of the body above the surface were rotted away. There is some evidence that these mud deposits were due to river flood-plain action and that

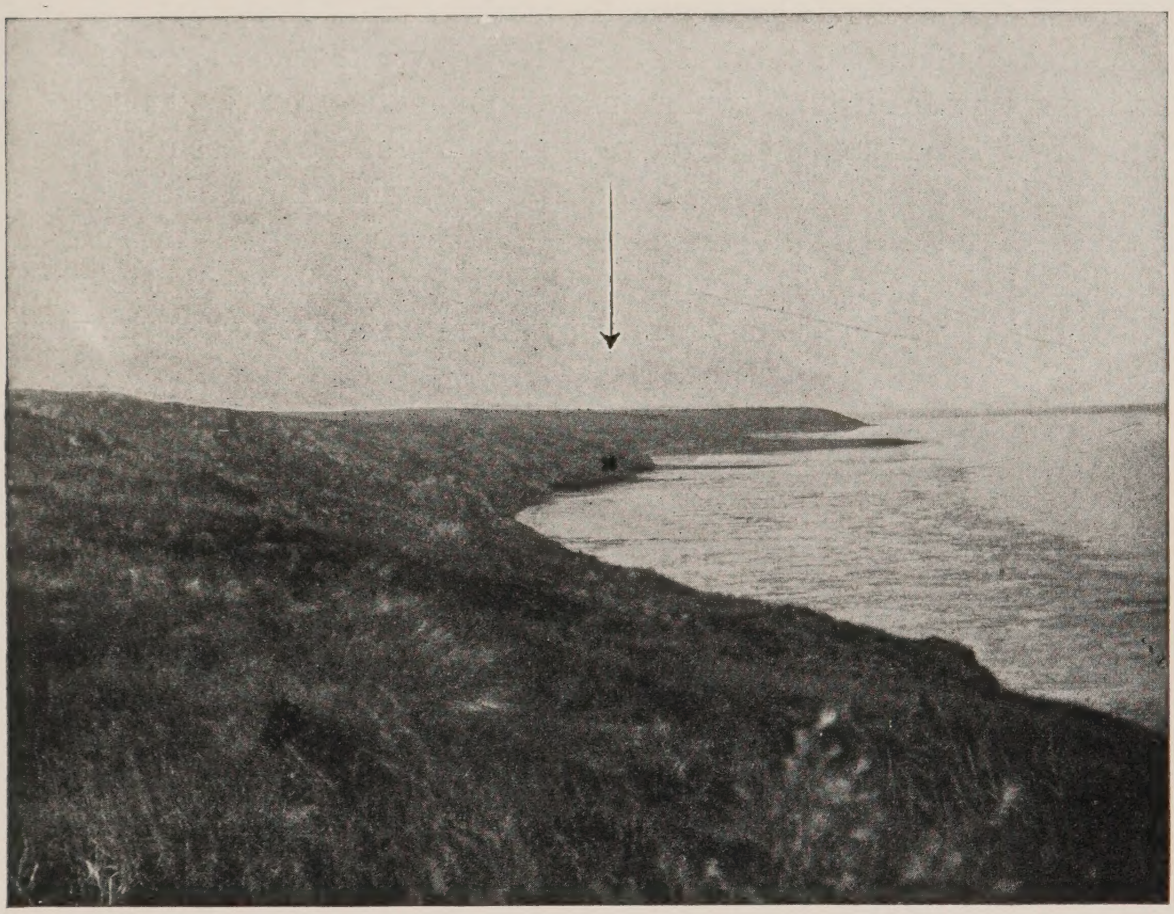


FIG. 216. — Bluff on the south side of Eschscholtz Bay, Alaska, where remains of many Pleistocene mammals have been found ('big bone beach'). The cross indicates the spot where part of a mammoth skeleton with some skin and hair was discovered. After Quackenbush, American Museum Expedition, 1908.

a part of the deposits have since become frozen. All are now covered by the thick vegetation of the tundras except where exposed at the seashore and along river borders.

The contemporaneity of these Alaskan species is by no means demonstrated. They may represent several successive periods of Pleistocene time: the moose and reindeer in the forests, the horses and bison (typical grazers) grazing on the uplands, the elephants and rare mastodons grazing and browsing in the forest borders, the beaver building their dams from the forests along the streams. The musk oxen and caribou, adapted to the mosses and shrubs of the barren grounds, are indicative of different periods.

Certainly the horse, the bison, and the elephants would have been

favored by a dry or arid climate, even if cold. Dall[1] remarks that the elevation of the continental shelf under Behring Sea about 300 feet would have laid bare an enormous level plain covering most of the present area of Behring Sea. The diminished body of water in connection with the prevalence of the northwest trade winds would have given to this region such a dry climate as characterizes much of Siberia and the Yukon Valley in Alaska to-day, which actually suffers from severe summer droughts.

Vast shallow lakes of muddy water might, as now happens in the same region, freeze solidly to the bottom and be covered with deposits of clay from the spring freshets, a condition explaining the great ice lenses of the 'ground ice' formation. Certain mammals might have been trapped in the quagmires formed by these clays. Finally, with the subsidence of the coast and the return of a milder climate, the ice lenses in the more northern and colder regions, especially where protected by the clays, by the freezing of the soil, and by the arctic vegetation, would be conserved to the present day.

Characteristic Mammals of the Third or Ovibos Zone

Distribution of musk oxen. — Beside the extinct short-horned musk ox (*Symbos*) found in Arkansas, remains of musk oxen are recorded[2] at Fort Gibson, Indian Territory, in three localities in Missouri, in Trumbull County, Ohio, at Big Bone Lick, Kentucky, in two localities in Pennsylvania, at Council Bluffs, Iowa, and near Salt Lake City, Utah. In every instance the remains have been recovered either directly from glacial deposits or from deposits that may be correlated with some stage of the Glacial Period. The skull of a musk ox (*Ovibos cavifrons*), discovered in part of the glacial terrace near the Ohio River in West Virginia, one mile from Steubenville, was associated with the shoulder blade of a mammoth of undetermined species. The reasonable inference seems to be that the musk oxen moved southward before the advancing ice, and then retreated northward to their present areas of distribution. (See Fig. 214.)

Cervalces. — An almost complete skeleton of an extinct moose was discovered in 1884 in the shell-marl deposit under a bog at Mt. Hermon, New Jersey, and described by Scott in 1885.[3] Its occurrence so far south of the present range of the moose points to a cold climate in New Jersey, but whether this animal belongs to the Megalonyx or to the Ovibos Zone cannot be determined at present. It is a remarkably long-limbed form, perhaps in adaptation to its habitat in snowy regions. The unusual size of the lateral digits would also favor the supposition of walking in the snow, although they may have been an adaptation to swampy conditions. The antlers are large and

[1] Dall and Harris, *op. cit.*, p. 266.

[2] Hatcher, J. B., Discovery of a Musk Ox Skull (*Ovibos cavifrons* Leidy), in West Virginia, near Steubenville, Ohio. *Science*, n.s., Vol. XVI, Oct. 31, 1902, pp. 707–709.

[3] Scott, W. B., *Cervalces americanus*, a Fossil Moose, or Elk, from the Quaternary of New Jersey. *Proc. Acad. Nat. Sci. Philadelphia*, 1885, pp. 181–202.

palmate, and are especially distinguished by broad inferior horizontal plates.[1] The animal, like the moose, was undoubtedly a tree-browser; the neck is so short in comparison with the limbs that the muzzle could not have been brought within fourteen or fifteen inches of the ground. To compensate for this the animal had a prehensile upper lip, which, however, was less pronounced than that of the moose. As in the moose, the withers are higher

FIG. 217. — The American deer-moose *Cervalces*. Restoration from a skeleton in the Museum of Princeton University. After original by Charles R. Knight in the American Museum of Natural History.

than the rump. *Cervalces* was a contemporary of the moose, which survived into recent times.

Sirenians, or sea-cows. — On both the Pacific and Atlantic coasts in Pliocene and Pleistocene times the most characteristic littoral mammals were the sirenians, or sea-cows, which were either derived from the migration of Old World forms from Africa by way of the north Pacific and Asia, or were descendants of a transatlantic (*Atlantis*) migration (p. 340) in Eocene times which found ready access to the Pacific coast through one of the great sea routes which separated North and South America as late as the Pliocene period. In favor of the theory of north Pacific migration is the striking similarity which exists between the Japanese and Californian

[1] On comparing the antlers of *Cervalces* with those of the moose, it becomes evident that the former consist of the same parts, with something added. Just what these additional parts are is by no means easy to say. *The anterior tine (of the ear-shaped process)* may be *the bez-antler, while the posterior one may correspond to the tine* which in *Megaceros*, the fallow-deer, and some others, is given off from the hinder surface of the beam nearly opposite the bez-antler. (Scott, 1885.)

representatives of the remarkable Pliocene mammal known as *Desmostylus* (see p. 344). Favoring the less probable theory of transatlantic migration from the African coast is the presence in supposed Eocene deposits of Jamaica of one of the most primitive of sirenians, the *Prorastomus* of Owen.[1] This animal, with its comparatively straight or normal upper jaw and complete series of teeth, is even more primitive in structure than the *Eosiren libyca* of the Upper Eocene Mokattam limestones (Fig. 89) of the Cairo and Fayûm districts of Africa.

The great northern sea-cow of the Pacific (*Rhytina stelleri*), or Steller's sea-cow, was discovered by Steller, who accompanied Behring on his last expedition of 1741 in search of the northwest passage.[2] It inhabited the shallow waters immediately surrounding certain of the Aleutian Islands, and moved by means of two small anterior flippers, which were covered with bristles, and by its fluked tail. The short fore leg terminated abruptly without fingers or nails, but was overgrown with a number of short, thickly placed brush hairs. It was a bulky animal, thirty or even thirty-five feet in length, and twenty feet in girth, weighing about 6,700 pounds, and covered with a very thick, much wrinkled skin of a dark brown color. Of all the Sirenia it was the only one adapted by its thick undercoating of blubber to inhabit the cold seas of the north. In Pleistocene times it probably ranged much farther south than the Aleutian Islands. It probably became extinct toward the end of the eighteenth century because it fell an easy prey to the sailors and fur traders.

Antiquity of Man in North America

The time of the first appearance of man on the North American continent still remains to be determined, and is a problem of the very highest importance.

Was man contemporaneous with the closing period of the second or *Megalonyx* fauna, or with the third, the *Ovibos* and late *Mastodon*, fauna? Did man enter this country from Asia or from South America? Are traces of human occupation found first on the Pacific or on the Atlantic coast? All these are questions which remain yet to be answered positively.

In brief, it may be said certainly, so far as anatomical evidence is concerned, that no trace of human skeletons of the Palæolithic or Neandertal type of Europe have been found in North America, and as certainly that all skeletons which have been reported have been referred finally to the recent Indian type. Second, there is some evidence of the coexistence of man with the late stages of the Megalonyx Zone in California and in the

[1] Owen, R., On *Prorastomus sirenoides*. *Quart. Jour. Geol. Soc. London*, Vol. XXXI, 1875, p. 559, Pl. 18 and 19.

[2] Nordenskiöld, A. E., The Voyage of the Vega round Asia and Europe, with a Historical Review of Previous Journeys along the North Coast of the Old World. Translated by Alexander Leslie. New York, 1882.

central states, as well as considerable evidence of the appearance of man before the disappearance of the mastodon in the eastern states. This raises the further question as to the period of the final extinction of the mastodon.

It will be interesting to pass in review some of the alleged or actual cases of the association of implements of human manufacture with the remains of various extinct mammals.

Man and the mastodon. — As early as 1839 flint arrowheads were reported by Koch in association with the bones of *M. americanus* in Missouri. Again, evidence for the contemporaneity of man and the mastodon was reported in the Pleistocene near Charleston by Holmes in 1859 and in the Pleistocene of California by Whitney (1866–1867). In 1869, however, Leidy declared [1] that neither of these alleged associations established beyond doubt the coexistence of man with any of the extinct Pleistocene mammals. In 1885, however, Putnam reported the remains of man and mastodon in Worcester, Massachusetts,[2] as follows: a mastodon tooth and a human skull were found associated together in a marsh eighteen feet below the surface; the lower jaw was embedded in blue clay; both showed that they had been transported by running water, and brought to this deposit before the overlying peat formation began. Norris, of the Bureau of American Ethnology, reported some fragments of elephant or mastodon tusks exhumed from a mound in Wisconsin. In 1887 Scott summed up the evidence as follows:[3] "It is well known to archæologists that pipes of catlinite shaped like the elephant have been discovered in Iowa, also that a so-called 'elephant mound' in Wisconsin has been much debated, since it is situated in the region of the effigy mounds of the northwest. . . . The coexistence of man and the mastodon, or mammoth, in America, as in Europe, has advanced now beyond the stage of presumption; it has been so well verified that it can hardly be excluded from the realm of science." Still, it is necessary to exercise care in the use of facts brought to light which seem to bear on this question. In 1887 D. G. Brinton [4] reported human footprints in the volcanic tufa at Lake Managua, about ten feet above which were mastodon remains. A striking feature of these footprints is that the second toe is the longest of all.

In 1895 Mercer [5] reported at Petit Anse, Louisiana, the discovery of modern implements, fourteen feet below the surface, underlying remains of an extinct elephant. This author considers that this may be a case of

[1] Leidy, J., The Extinct Mammalian Fauna of Dakota and Nebraska, Including an Account of Some Allied Forms from Other Localities, together with a Synopsis of the Mammalian Remains of North America. *Jour. Acad. Nat. Sci. Phila.*, (2) Vol. VII, 1869, pp. 1–472.

[2] Putnam, F. W., Man and the Mastodon. *Science*, Vol. VI, no. 143, 1885, pp. 375–376.

[3] Scott, W. B., On American Elephant Myths. *Scribner's Magazine*, Vol. I, April, 1887, p. 469.

[4] Brinton, D. G., On an Ancient Human Footprint from Nicaragua. *Proc. Amer. Phil. Soc. Phila.*, Vol. XXIV, 1887, pp. 437–444.

[5] Mercer, H. C., The Antiquity of Man at Petit Anse (Avery's Island), Louisiana. *Amer. Natural.*, Vol. XXIX, no. 340, April, 1895, pp. 393–394.

'intrusive burial,' in which a grave was dug down through the earth to the salt. Another case of obviously artificial or accidental association is that reported in a sulphur spring at Afton, Indian Territory, by Holmes[1] (1901), where flint arrowheads and other implements were found in association with teeth and other remains of mammoth (probably *E. primigenius, E. imperator*), fossil bison, and the horse. The most plausible explanation of this accumulation is that the spring was regarded as magical by the Indians, who threw into it not only such fossil bones as were exposed in the vicinity, but also their most precious possessions, including their various weapons and implements.

By far the most authentic case is that reported by Clarke[2] in 1903. A small tusk, ribs and other bones of a young mastodon were found at Attica, Wyoming County, New York, in unlaminated clay overlaid by muck, etc., at a depth of two to three feet. Several pieces of charcoal were discovered under these bones, and in another part of the same swamp and one foot below the level of the bones, some bits of broken pottery and a considerable quantity of charcoal were discovered.

Man and Megalonyx. — At Natchez, Mississippi, a human pubic bone was found in 1846 in association with a true Megalonyx fauna. The bones were reported to be in the same condition of preservation as the larger bones, and hence may be considered contemporary.[3] Leidy considered that this pelvic bone might have fallen in from one of the Indian graves above it. Wilson,[4] however (1892), reported that a chemical investigation of the human bone showed it was more advanced in fossilization than that of the associated *Mylodon*, and hence might be considered as old or older. Cope (1895)[5] rejected the previous evidence, stating that no trace of man had been found in the Megalonyx fauna.

In 1896, however, Mercer[6] expressed the opinion that the remains of *Megalonyx* found in the Big Bone Cave, Van Buren County, Tennessee (Fig. 194, 10), were not appreciably older than the associated human remains. This is by far the most significant of these associations, and is more fully described below (p. 498).

The most recently discovered associations of *Megalonyx* with supposed artifacts of human manufacture are in the Potter Creek and Samwel caves,

[1] Holmes, W. H., Flint Implements and Fossil Remains from a Sulphur Spring at Afton, Indian Territory. *Ann. Rept. U.S. Nat. Mus.*, 1901, pp. 233–252.

[2] Clarke, J. M., Mastodons of New York. A List of Discoveries of their Remains, 1705–1902. *N.Y. State Mus. Bull.*, 69, Palæontology, 9, 1903, p. 932.

[3] Leidy, 1869.

[4] Wilson, T., Man and the Mylodon. Their Possible Contemporaneous Existence in the Mississippi Valley. *Amer. Natural.*, Vol. XXVI, no. 307, July, 1892, pp. 628–631.

[5] Cope, E. D., The Antiquity of Man in North America. *Amer. Natural.*, Vol. XXIX, 1895, pp. 593–599.

[6] Mercer, H. C., Cave Exploration by the University of Pennsylvania in Tennessee. *Amer. Natural.*, Vol. XXX, no. 355, July, 1896, pp. 608–611; also, Cave Exploration in the Eastern United States, Preliminary Report. *Dept. Amer. Prehist. Archæol. Univ. Pa.*, 1896.

the fauna of which is described above (p. 476). The weight of this evidence may be estimated from the opinions of Putnam (1905) and of J. C. Merriam (1906) cited below.

Human implements and extinct mammals. — None of the early reports of association afford unequivocal evidence: the arrowheads found by Koch in 1839 in association with the bones of mastodon, those reported by Mercer, those in the sulphur spring at Afton (Indian Territory), all appear to be cases of accidental association. The flints and obsidian artifacts found in Fossil Lake, Oregon, with the mammals of the Equus fauna are also apparently an entirely superficial association.

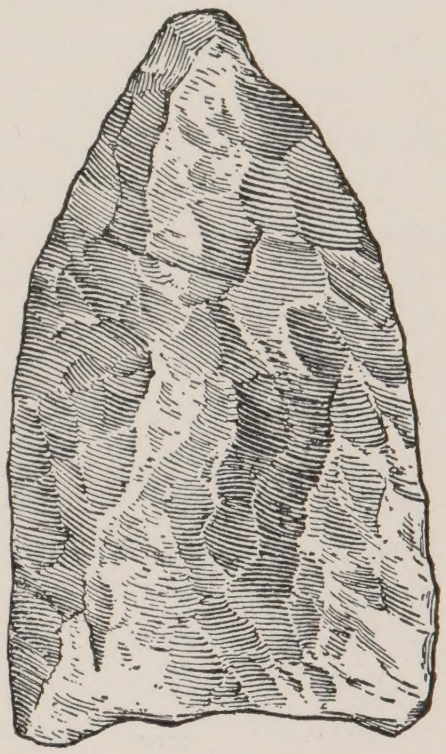


Fig. 218. — Flint arrow-head discovered under skeleton of *Bison antiquus* in the Pleistocene of Kansas. After Williston.

The most important case of association of an arrowhead with an extinct species of bison is that reported by Williston.[1] As above described (p. 464), underneath the scapula of an extinct species of bison (*B. occidentalis*) an arrowhead was found imbedded in the matrix, but touching the bone itself. The arrowhead must have been within the body of the animal at the time of death or lying on the surface beneath its body. At no great distance from this point bones of the elephant (*E. columbi*) have been found in the same material, namely, in the widespread upland marl which covered these skeletons.

Russell[2] describes the discovery of a spearhead in the 'upper lacustral clays' of the Lahontan basin as follows: "The fossil from the Lahontan Basin, which will probably be considered by both geologists and archæologists as of the greatest interest, is a spearhead of human workmanship. This was obtained by Mr. McGee,[3] from the upper lacustral clays exposed in the walls of Walker River Cañon, and was associated in such a manner with the bones of elephant or mastodon, as to leave no doubt as to their having been buried approximately at the same time. Both are genuine fossils of the pre-Lahontan period. The spearhead is of chipped obsidian, and is in all respects similar to many other implements, commonly found on the surface, throughout the far West."

The most recent of these associations is the alleged evidence of man's

[1] Williston, S. W., An Arrow-head found with Bones of *Bison occidentalis* Lucas, in western Kansas. *Amer. Geol.*, Vol. XXX, Nov., 1902, pp. 313–315.

[2] Russell, I. C., Geological History of Lake Lahontan. A Quaternary Lake of Northwestern Nevada. *Monogr. U.S. Geol. Surv.*, Vol. XI, 1885.

[3] W J McGee, the well-known geologist and ethnologist.

handiwork in the Shasta Caves (Potter Creek and Samwel) of California, which contain a pure though late Pleistocene fauna. Examination by Putnam[1] led him to the conclusion that the evidence of man's handiwork, consisting chiefly of two perforated bones, is sufficiently important to warrant belief that man lived in the vicinity of these caves. Merriam,[2] however (1906), adopted the somewhat more conservative conclusion that the "splintered, polished, perforated fragments of bone, etc., found in the Potter Creek and Samwel caves look like human artifacts, but cannot be pronounced such with certainty at present."

Human remains in cave deposits. — It is noteworthy that while the European cave deposits are of late Pleistocene age, frequently containing remains of man, American caves are chiefly of mid-Pleistocene age, and not until we reach the Potter Creek (p. 475) and Samwel caves (p. 477) in California do we find any evidence, and that not conclusive, of the existence of man.

In the East this has been made a subject of special investigation by Mercer.[3] His journey of six hundred miles was especially directed to those mountain passes and river ways by which early man may have first penetrated the great forests of the Appalachians in traveling from the Pacific coast and plains region of the West. In every case investigated along the Tennessee, Ohio, and Kanawha rivers in Ohio, West Virginia, Indiana, and Kentucky, remains of man were found associated only with the recent fauna such as the deer, gray fox, raccoon, opossum, black bear, turkey, etc.

The only exception was the Big Bone Cave, Van Buren County, Tennessee, where nine hundred feet from the entrance were found remains of the fossil sloth, megalonyx, fresh in appearance, with remains of the cartilages attached, associated with fragments of reeds which had apparently been used as torches by Indians, thus presenting evidence of the contemporaneity of the modern Indian with the extinct megalonyx. This evidence convinced Mercer that at least in the eastern valley of Tennessee at a height of six to seven hundred feet above sea level man coexisted with the great sloth. Again, in Zirkel's Cave, Jefferson County, Tennessee, two faunal levels were discovered, the lower containing the tapir, peccary, and bear, the upper containing the marmot, or woodchuck (*Marmota*), opossum (*Didelphys*), rabbit, and cave rat associated with Indian remains. This appears to be the first instance thus far discovered in eastern North America of the occupation of caves by man, and of a modern fauna overlying an ancient fauna. The second instance is that of Look Out Cave on the left

[1] Putnam, F. W., Evidence of the Work of Man on Objects from the Quaternary Caves in California. *Amer. Anthropol.*, n.s., Vol. VIII, 1905, pp. 229–235.

[2] Merriam, J. C., Recent Cave Exploration in California. *Amer. Anthropol.*, n.s., Vol. VIII, no. 2, Apr.–June, 1906, pp. 221–228.

[3] Mercer, H. C., Cave Exploration in the Eastern United States. *Dept. Amer. Prehist. Archæol., Univ. Penn.*, July 4, 1894; Cave Exploration in the Eastern United States. *Dept. Amer. Prehist. Archæol., Univ. Penn.*, June 4, 1896.

bank of the Tennessee River, containing bones of the tapir and mylodon in in the lower zone, and Indian remains in an upper zone of black earth.

Skeletal Remains Attributed to Early Man

We owe to Hrdlička [1] a thorough comparative study of all the skeletal remains which have been discovered in North America and attributed to early man. He observes that proof of the geological antiquity of human remains demands indisputable stratigraphic evidence, some degree of fossilization, and marked anatomical distinctions in the more important parts of the skeleton. A skeleton which agrees with that of a recent or not very ancient race in the same locality cannot be accepted as geologically ancient unless the geological evidence be absolutely decisive.

Since 1844 fourteen discoveries have been made with more or less serious claim of considerable geological antiquity. Of these the chief are the Natchez (Mississippi) pelvic bone (1846), the Calaveras (California) skull (1866), the Trenton (New Jersey) skulls (1879, 1887), the Lansing (Kansas) skeleton (1902), and the Nebraska 'loess man' (1894, 1906).

In some instances association of the human bones with those of extinct animals is due to 'intrusive burials,' *i.e.* burials in which the grave happened to be carried below the level of a stratum containing a number of extinct forms. The Natchez pelvic bone may be a case of accidental association of a bone fallen from an Indian grave and mingled with older fossilized bones. The famous Calaveras skull agrees closely with the cave skulls from Calaveras County geologically of recent age. The Trenton crania found in glacial gravels along the Delaware River are of doubtful geological age, while their anatomical characters are not those of the Delaware Lenape Indians recently inhabiting the district, but appear of relatively modern and European origin. The Lansing skeleton found twenty feet below the surface in the loess-like silt was heralded as a find of real geologic antiquity, but proves to agree closely with the typical upper Mississippi valley Indian of the present day. Similarly, the fossil human bones from the west coast of Florida show a marked anatomical likeness to recent Indian bones. The Nebraska loess man, which was regarded by the present writer (Osborn) and others as exceptionally primitive, proves to correspond in its low forehead with certain low-type Indian crania, such as are found among the mound-builders of Arkansas and even among certain recent Indians.

"Under the circumstances," concludes Hrdlička, it must be stated that "thus far on this continent no human bones of undisputed geologic antiquity are known," and anatomically the remains indicate their affinity or identity with those of modern Indians. This does not mean that early man did not

[1] Hrdlička, A., Skeletal Remains Suggesting or Attributed to Early Man in North America. *Smiths. Inst., Bur. Ethnol., Bull.* 33, 1907.

exist in North America, but that convincing proof of the fact from the standpoint of physical anthropology still remains to be produced.

Auriferous gravels. — The most recent review of this question is that of Sinclair,[1] in which the following conclusion has been reached: "A review of the evidence favoring the presence of the remains of man in the auriferous gravels of California compels one to regard it as insufficient to establish the fact. It has been shown either that there have been abundant opportunities for the relics in question to be mixed with the gravels accidentally, or that the geological conditions at the localities are such as to render it improbable that the implements and bones have been associated in the gravels to the extent supposed."

Mercer[2] reached a negative conclusion in his survey of the Trenton gravels: "Nor has anything yet been found anywhere else in the valley to corroborate the alleged antiquity of the chipped blades from Trenton." The Trenton case has been somewhat weakened by the appearance among the drift specimens of several blades of common Indian pattern.

Causes of Pleistocene Extinction[3]

Certainly the most direct instance of widespread extinction of quadrupeds contemporaneous with a secular change of climate was that of the Glacial Period in the entire northern hemisphere.

As we have seen, the beginning of the Pleistocene found North America peopled with the following kinds of great quadrupeds, all of which disappeared during or shortly after the Ice Age:

Artiodactyla	Camelidæ	Camels
		Llamas
Perissodactyla	Equidæ	Horses
	Tapiridæ	Tapirs
Proboscidea	Mastodontinæ	Mastodons
	Elephantinæ	Elephants
Edentata	Gravigrada	Giant Sloths
		Megalonyx
		Megatherium
		Paramylodon
	Glyptodontia	*Glyptotherium*

It would be natural to assume that extinction was *directly* brought about by the profound changes of temperature and moisture, accompanied by

[1] Sinclair, Wm. J., Recent Investigations bearing on the Question of the Occurrence of Neocene Man in the Auriferous Gravels of the Sierra Nevada. *Univ. Cal. Publ., Amer. Archæol. Ethnol.*, Vol. VII, no. 2, 1908, pp. 107–131.

[2] Mercer, H. C., The Antiquity of Man in the Delaware Valley. *Repr. fr. Publ. Univ. Pa.*, Vol. VI, 1897, pp. 1–85.

[3] Osborn, H. F., The Causes of Extinction of Mammalia. *Amer. Natural.*, Vol. XL, no. 479, Nov., 1906, pp. 769–795, no. 480, Dec., 1906, pp. 829–859.

changes in the fauna and flora consequent upon the great geologic and physiographic changes of Glacial times; but this simple explanation is beset with many difficulties and contradictions, and the results must be analyzed with some care. The extinction of the horse in North America, for example, does not admit of such a simple explanation.

While in Europe the Mediterranean Sea presented a barrier to escape or migration to the south, in North America there were broad continental

FIG. 219. — **Holocene or Recent times.** A period of continental depression. Asia and North America completely separated, preventing further intermigrations of mammals. The island systems of the New and Old Worlds and of Australia mostly separated. Africa united with Europe by a narrow desert strip, a barrier to further migration.

areas and high plateaux affording easy migration routes southward, and every means of escape.

It is, therefore, more in accord with the facts to say that the Glacial Period in North America originated certain new conditions of life which directly or indirectly resulted in extinction.

These conditions include diminished herds, enforced migrations, the possible overcrowding of certain southerly areas, changed conditions of feeding, disturbances in the period of mating and reproduction, new relations with various enemies, aridity, and deforestation; in short, a host of indirect causes.

Protective adaptation to secular cold. — The resistance of mammals to cold depends upon (*a*) the internal heat-producing power, which is a progressive adaptation of the higher Mammalia, correlated with (*b*) the accession of a warm external covering in the form of hair, wool, or blubber

as in the case of aquatic mammals. The well-known cases of adaptation to extreme cold among elephants (*E. primigenius*, woolly mammoth), rhinoceroses (*R. antiquitatis*, woolly rhinoceros), steppe camels of Asia (*Camelus bactrianus*), steppe horses (*Equus przewalskii*), and steppe antelopes (*Saiga tartarica*) indicate that we must not assume that cold was in all cases the direct cause of extinction.

Cold and the numerical diminution of herds. — As suggested by Darwin, a *temporary diminution* in numbers, whether caused by cold waves, long or repeated droughts, floods, epidemics, or other unfavorable conditions of life, may indirectly lead to extinction. The protection of a herd of animals from hostile Carnivora often depends on its numbers. It has been observed recently that the woodland bison (*B. athabascæ*) of British Columbia is in danger of extinction because the bulls are not sufficiently numerous to protect the young. Numerical diminution may in this way become a cause of extinction.

The observations of Prichard [1] in Patagonia give an interesting instance of the influence of severe winters on the very hardy guanacos and deer of that region.

"Around the lake lay piled the skulls and bones of dead game, guanaco (*Lama huanachus*) and a few huemules (*Furcifer chilensis*). These animals come down to live on the lower ground and near unfrozen water during the cold season, and there, when the weather is particularly severe, they die in crowds. We saw their skeletons in one or two places literally heaped one upon the other" (*op. cit.*, p. 132). "Again we came upon a second death-place of guanaco, which made a scene strange and striking enough. There cannot have been less than five hundred lying there in positions forced and ungainly as the most ill-taken snapshot photograph could produce. Their long necks were outstretched, the rime of the weather upon their decaying hides, and their bone-joints glistening through the wounds made by the beaks of carrion-birds. They had died during the severities of the previous winter, and lay literally piled one upon another" (*op. cit.*, p. 189). "The meaning of this I gathered from Mr. Ernest Cattle. He told me that in the winter of 1899 enormous numbers of guanaco sought Lake Argentino, and died of starvation upon its shores. In the severities of winter they seek drinking-places, where there are large masses of water likely to be unfrozen. The few last winters in Patagonia have been so severe as to work great havoc among the herds of guanaco" (*op. cit.*, p. 255).

Diminished herds and inbreeding. — Another danger attending diminished herds in restricted regions is close inbreeding. On this familiar subject see Gerrit S. Miller's [2] paper "Fate of the European Bison Herd," in which the author shows the possibly fatal influence of inbreeding on diminished herds, although it must be pointed out that these bison are protected and are thus *living under unnatural conditions.*

[1] Prichard, H. H., Through the Heart of Patagonia. New York, 1902.

[2] Miller, G. S., Jr. The Fate of the European Bison Herd. *Science*, n.s., Vol. IV, no. 99. Nov. 20, 1896, pp. 744–745.

In a paper entitled "Das allmähliche Aussterben des Wisents (*Bison bonasus*, Linn.) im Forste von Bjelowjesha," [1] Mr. Eugen Büchner gives a detailed history of the bison herd in the Bieloviejsha (or Bialowitza) forest, Province of Grodno, in Lithuania, Russia, during the present century. "A careful study of the breeding habits of the bison in the Bieloviejsha forest and elsewhere leaves no room for doubt that the present slow rate of reproduction is an abnormal condition, and that to it is due the rapid approach of the extinction which is the certain fate of the herd under consideration. This diminished fertility the author regards as a stigma of degeneration caused by inbreeding. . . . Another indication of the degenerate condition of the Bieloviejsha herd is seen in the great excess of bulls, which probably outnumber the cows two to one. This is doubtless a result of inbreeding, for Düsing [2] has shown that close inbreeding, like a reduced condition of nutrition, is favorable to the production of an excess of males. . . . In conclusion, the author considers that his studies of the history of the Bieloviejsha bison leave scarcely room for doubt that inbreeding is the cause of the final extinction of most large mammals. Inbreeding must begin and lead gradually but certainly to the extinction of a species when it, through any cause, has become so reduced in numbers as to be separated into isolated colonies."

Influence of cold during the reproduction period. — Exceptional cold waves or unusually prolonged cold seasons may cause a temporary loss of food supply or cause the death of the young, which in northern latitudes are usually born in spring. The diminution or loss of young from this cause might act as the first of a series of destructive effects of a progressive secular change. These may be summarized as follows from the actual observations [3] of zoölogists upon the Cervidæ: (*a*) disturbed conditions during the conjugation (pairing, mating, rutting) period; (*b*) enfeebled (through hunger) condition of females during parturition period; (*c*) severe weather conditions, ice storms, crusted snow, prolonged wet and sleet at time of birth; (*d*) bulls unable to protect herds; (*e*) cows unable to protect young from Carnivora through starved condition, or abandoning them when attacked by wolves; (*f*) enfeebled and unprotected condition of quadrupeds favorable to increased food supply and consequent multiplication of cursorial and other Carnivora, especially Canidæ and Felidæ.

These zoölogical observations are to a certain extent borne out in palæontology by Leith Adams' ("British Fossil Elephants," 1879, Pt. 2, p. 98) observations of the exceptionally large number of milk teeth of elephants found in certain Pleistocene deposits, which appears to indicate a high mortality of the young. (See also Holland, p. 471.)

[1] Büchner, Eugen, *Mém. Acad. Impér. Sci. St. Pétersbourg*, Vol. III, no. 2, 1895, pp. 1–30.

[2] Düsing, *Jen. Zeitschr. Naturwiss.*, Vol. XVII, 1884, p. 827.

[3] Communicated by Mr. Madison Grant, Secretary of the Zoölogical Society of New York.

Temperature control of fertility and reproduction. — Merriam [1] has directed attention to one of the physiological effects of a lowering of temperature, namely, its influence upon diminished or increased fertility and the rate of reproduction in what he has called the 'law of temperature control.' This he has stated as follows: temperature by controlling reproduction predetermines the possibilities of distribution; it fixes the limits beyond which species cannot pass; it defines broad transcontinental barriers within which certain forms may thrive if other conditions permit, but outside of which they cannot exist, be the other conditions never so favorable (because the sexes are not fertile).

Temperature and geographic range. — In discussing how species are checked in their efforts to overrun the earth Merriam points out that more important than geographic barriers are the *climatic barriers* (as observed by Humboldt), and of these that temperature is more important than humidity. First, in 1892, this author attempted to show [2] that the distribution of terrestrial animals is governed less by the yearly isotherm or mean annual temperature than by the total rather than the mean temperature during the period of reproductive activity and of growth (adolescence). This reproductive period in the tropics extends over many months or nearly the whole year, and within the Arctic Circle and summits of high mountains is of two months or less duration. Later, in 1894, results which Merriam [1] obtained from extensive comparison of temperatures and distribution justified the belief that animals and plants (Lower Austral and tropical types coming from the South) are restricted in northward distribution by the total quantity of heat during the season of development and reproduction. Conversely animals and plants (Upper Austral, Transition, and Boreal types coming from the North) are restricted in southward distribution by the mean temperature of a brief period covering the hottest part of the year. Thus in the Transition Zone, Boreal and Austral types mingle in the equable climate of the Pacific coast of California, while they are sharply separated by the inequable extremes of cold and heat of the interior continental plateau.

It follows from these observations that animals forced out of their natural habitat may become extinct through infertility.

Influence of cold and snow on food supply and choice of food. — It is probable that during the Glacial Period the great winter snow blanket covering the natural food supply, rather than the direct influence of the cold itself, was one of the chief causes of extinction. The death of great numbers of animals from hunger or starvation through the covering of food during the winter season under heavy layers of snow is commonly observed among

[1] Merriam, C. H., Laws of Temperature Control of the Geographic Distribution of Terrestrial Animals and Plants. *Nat. Geogr. Mag.*, Vol. VI, Dec. 29, 1894.

[2] Merriam, C. H., The Geographic Distribution of Life in North America with Special Reference to the Mammalia. *Proc. Biol. Soc. Washington*, Vol. VII, Apr. 13, 1892, pp. 45–46.

FIG. 220. — Pliocene and Pleistocene extinction. Former (*ruled lines*) and recent (*solid black*) distribution of: A. Rhinocerotidæ, rhinoceroses. B. Proboscidea, elephants and mastodons. C. Equidæ, horses, asses, and zebras.

the large herds of the domesticated horses and cattle on the western plains. Under these conditions horses are driven to food, such as the branches of willows, which is very deleterious to them. Under the influence of hunger cattle will also feed eagerly and indiscriminately on plants which may be injurious to them or to their young, as recorded by Chestnut and others in the United States Agricultural Department. After heavy snowstorms, when the grass is covered with snow, it often happens that only the taller species of plants are exposed.[1] In such cases the poisonous larkspurs (*Delphinium glaucum*) are greedily eaten by cattle which would otherwise avoid these plants. This tendency is increased by the fact that ruminants do not feel at ease so long as the stomach is not full, and are inclined to eat anything in sight after a snowfall.

Similarly, enforced migrations among wild as among domesticated animals might cause them to become less fastidious about their food. It is observed[1] among domesticated animals that when feeding quietly on the range they exercise considerable choice in the selection of forage plants, but when driven six or eight miles daily they are frequently forced by hunger to bite off almost all kinds of plants which grow along their course. Animals vary greatly in adaptability to new conditions caused by long cold and heavy snowfall; horses remove snow even to a depth of three or four feet, and find food sufficient to carry them through the winter, while cattle under the same conditions starve.

Forestation, deforestation, and reforestation. — It is certain that the Holarctic region, or circumpolar belt, was forested even to the shores of the Arctic Ocean in early Pleistocene times. The remains of large extinct quadrupeds in this region are almost everywhere associated with evidences of forests, and of forest-frequenting animals, such as the beaver. The forests naturally furnished the necessary conditions of life of certain quadrupeds, especially of browsing animals, and even of Proboscidea. Among Artiodactyla the deer, among Perissodactyla the tapirs, are typical forest animals. Conditions, therefore, which would cause deforestation would also become the means of diminution, and finally of extinction. Such conditions are intense cold, (*a*) heavy snow-capping of the tundra regions of the north, (*b*) the dry cold and dust storms of the steppes. In Europe a period of deforestation and a long unforested period of dry cold certainly succeeded each other. In North America we have evidence of similar conditions in our own loess period, and there certainly occurred a great deforestation in the regions now known as the 'barren grounds,' which pass into the tundras with frozen subsoil to the north.

After considering the diminution of life in Alaska, Maddren[2] summarizes

[1] Chestnut, V. K., The Stock Poisoning Plants of Montana. *U.S. Dept. Agric., Div. Botany.*, Bull. 26, Washington, 1901.

[2] Maddren, A. G., Smithsonian Exploration in Alaska in 1904, in Search of Mammoth and other Fossil Remains. *Smiths. Misc. Coll.*, Vol. XLIX, 1905, p. 65.

his conclusions as follows: that the most rational way of explaining the extinction in Alaska is the gradual change from more temperate conditions which reduced and finally destroyed the forest vegetation, thus reducing the food supply and reducing the fauna to those forms capable of adapting themselves to the recent tundra vegetation.

Extermination of horses. — Among all the problems of Pleistocene extinction presented in America, that of the horses is certainly one of the most difficult. These animals are far superior to cattle in their adaptability to changed conditions of life and in resourcefulness during severe winter seasons. They were extraordinarily numerous in North America at the beginning of the Pleistocene; at the close it appears that they were entirely extinct. Similar extinction occurred both in North and South America in Pleistocene times. It is consequently impossible to connect this phenomenon directly with the Ice Age. In Pleistocene times there was a ready escape to the high plateaux of Mexico, which must have presented all the most favorable conditions for equine life, of climate, soil, and food. The numerous and highly specialized horses of Mexico shared in this extinction. It has consequently been suggested by the writer and by others that the horses may have been swept out of existence by some epidemic disease or diseases. These diseases are carried by flies and are favored by moist conditions occurring chiefly during or immediately after heavy rainfalls, though in sporadic cases they may occur at other seasons of the year; such moist conditions occurred periodically in the Great Basin of Oregon and Nevada and in the valley of Mexico. The disease known in India as 'surra' has a widespread geographic distribution. In Africa there is a similar malady, 'nagana,' or tse-tse fly disease. In Algeria, France, and Spain the horse and the ass are both liable to the attacks of a trypanosome (*T. equiperdum*). In South America the *mal de caderas* affects horses, asses, cattle, and certain other animals, and is attributed to a trypanosome; it is distinctively a wet weather disease, almost completely disappearing in the dry seasons. The tse-tse fly of Africa renders thousands of square miles uninhabitable by horses. The rapid rate at which such diseases may travel is illustrated by the spread of the rinderpest, which traversed the whole length of Africa in fifteen years.

This theory of an epidemic among the American horses during the wet weather periods of Glacial times receives some support from the discovery by Cockerell in the Miocene insect fauna of Florissant, Colorado, of two species of tse-tse fly (*Glossina*) very similar to the African types. The application to the Pleistocene is that a moist or rainy period extending over the Southern States and down into Mexico during Pleistocene times would have favored the distribution of some flies or other parasite-bearing insects, such as ticks, and have resulted in the extinction of the horses.

Influence of increased rain supply. — Dry or moderately dry conditions, if not too extreme, are generally more favorable to quadrupeds than moist

conditions. The plains and forest regions most densely populated with quadruped life, such as those of the African plateaux of the present day, are regions of moderate rainfall and even of prolonged summer droughts. The regions less densely populated with quadrupeds are those of heavy rainfall, of dense forests and vegetation, such as those of the equatorial belt of South America or the Mango region of Africa. Moisture and temperature are, therefore, to be first considered in relation to forestation.

Increased rainfall has many other effects: (1) it may diminish the supply of harder grasses to which certain quadrupeds have become thoroughly adapted; (2) it may at the same time produce new poisonous or deleterious plants; (3) it may be the means of introducing new insects or other pests, and new insect barriers; (4) it may be the means of introducing new protozoan diseases and new insect carriers of disease; (5) it may be the means of erecting new forest barriers to migration, or new forest migration tracts for certain Carnivora, such as the bears.

It follows that periods of secular increasing moisture, such as the early and mid-Pleistocene of the northern hemisphere is supposed to have been, may have been unfavorable to certain large quadrupeds which had become adapted to Pliocene conditions of semi-aridity, even prior to the advent of extreme cold. As regards migration, Merriam observes that *humidity* is a less potent factor than temperature in limiting the distribution of the Mammalia of North America. Thus many genera adapted to certain restrictions of temperature ranged east and west completely across the American continent, inhabiting alike humid and arid subdivisions, but no genus adapted to certain conditions of *humidity* is able to range north and south across the temperature zones.

Food supply and moisture. — Sheep and cattle owners of the Northwest have observed that the majority of poisonous plants are those which flourish during moist seasons, such as the death camas (*Zygadenus*), the larkspurs (*Delphinium*), the water hemlocks (*Cicuta*), the white loco (*Aragallus*).

It is a matter of universal observation that in tick- or insect-infested countries dry seasons result in the reduction, moist seasons in the increase of diseases: dry localities are favorable; moist localities are unfavorable. Thus the tse-tse fly is not found in the open veldt; it must have cover. Warm, moist, steamy hollows containing water, inclosed with forest growth, are the haunts chosen.

Ticks, even when non-infection-bearing, form absolutely effective barriers to the introduction of quadrupeds into certain regions. In certain forested portions of South and Central America they endanger human life. In certain regions of Africa ticks are practically fatal to horses. As observed by Elliot, thousands of ticks would sometimes gather on a horse as the result of a single night's grazing. The mane especially serves to collect

these pests; thus the falling mane of the northern horse is distinctly disadvantageous as compared with the upright mane of the asses and zebras. Ticks abound in the southern plains region of the United States, as well as in the forests bordering the Mexican plateau, and are thus both plains and forest pests. They are certainly to be considered in connection with the extermination of horses.

OUTLINE CLASSIFICATION

OF THE

MAMMALIA

RECENT AND EXTINCT

INCLUDING ESPECIALLY THE BETTER KNOWN GENERA AND FAMILIES AND THOSE MENTIONED IN THIS BOOK

This classification has been prepared under the direction of the author by W. K. Gregory and Johanna Kroeber Mosenthal. The geological range and revision of the extinct genera has been done with the coöperation of W. D. Matthew. The scheme of classification under four grand divisions, and the order throughout, from the more ancient and primitive to the more specialized forms, is that of the author.

APPENDIX

LIST OF ABBREVIATIONS AND SYMBOLS

†	extinct.
Nom. nov. . . .	new (group) name.
Inc. Sed.	(*Incertæ Sedis*), of uncertain systematic position.
Fam.	family.
Bas.	Basal.
L.	Lower.
M.	Middle.
U.	Upper.
Trias. . . .	Triassic.
Jur.	Jurassic.
Cret.	Cretaceous.
Eoc.	Eocene.
Olig.	Oligocene.
Mioc. . . .	Miocene.
Plioc. . . .	Pliocene.
Pleist. . . .	Pleistocene.
Rec.	Recent.

In cases where the generally accepted name is preoccupied it is placed within quotation marks, and the technically correct name is placed after it in brackets, e.g. '*Echidna*' (=*Tachyglossus*).

Following is a list of the general works consulted in drawing up the classification. Works dealing with particular groups are cited below.

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Beddard, F. E. . . Mammalia. The Cambridge Natural History, Vol. X. London. 1902.

Cope, E. D. . . . . The Vertebrata of the Tertiary Formations of the West. *Rept. U.S. Geol. Surv.* (Hayden). Washington. 1884.

Depéret, C. . . . L'évolution des Mammifères tertiaires; importance des migrations. *C. R. Acad. Sci. Paris*, Vol. cxli, séa. Nov. 6, 1905; Vol. cxlii, séa. March 12, 1906; Vol. cxliii, séa. Dec. 24, 1906.
Transl. by Johanna Kroeber, *Amer. Natural.*, Vol. xlii, Nos. 494, 495, 497, Feb., March, and May, 1908, pp. 109–114, pp. 166–170, pp. 303–307.
[Latest and most authoritative review of Tertiary faunas of Europe.]

Elliot, D. G. . . . A Catalogue of the Collection of Mammals in the Field Columbian Museum. *Field Columbian Museum Publ.*, No. 115. Chicago, 1907.
The Land and Sea Mammals of Middle America and the West Indies. *Field Columbian Mus. Publ.*, 95. Chicago, 1904. [Very numerous illustrations, including drawings of the animals, and photographs of the skulls.]

FLOWER, W. H., and LYDEKKER, R. — An Introduction to the study of Mammals Living and Extinct. London, 1891. [Excellent generic descriptions of recent mammals.]

GREGORY, W. K. . . — The Orders of Mammals. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVII, 1910, pp. 1–524. [Part I treats history of the ordinal classification of mammals; Part II discusses the evolution and relationship of the orders.]

HAY, O. P. . . . . — Bibliography and Catalogue of the Fossil Vertebrata of North America. *Bull. U.S. Geol. Surv.*, No. 179. Washington, 1902. [A remarkably complete key to the literature of extinct mammals of America.]

HORNADAY, W. T. . — The American Natural History. New York. 1904. [Useful descriptions and illustrations, especially of American rodents, carnivores, and ungulates.]

KINGSLEY, J. S. . . — The Standard Natural History, Vol. V, Mammals. Boston. 1884.

LYDEKKER, R. . . . — A Geographical History of Mammals. Cambridge. 1896.
The New Natural History. Vols. I–III. New York.

OSBORN, H. F. . . — Evolution of Mammalian Molar Teeth. New York. 1907. [Figures the teeth of many extinct and recent genera.]
Cenozoic Mammal Horizons of Western North America, with Faunal Lists of the Tertiary Mammalia of the West by W. D. Matthew. *U.S. Geol. Surv.*, Bull. 361. Washington. 1908. [Numerous sections and maps. Faunal migrations and interchange with the Old World.]

PALMER, T. S. . . — Index Generum Mammalium. A List of the Genera and Families of Mammals. *U.S. Dept. Agric., Divis. Biol. Surv., No. Amer. Fauna*, No. 23. Washington, 1904. [Key to history of generic and family names.]

SCLATER, W. L., and SCLATER, P. L. — The Geography of Mammals. London. 1899. [Figures of rare modern genera.]

SCLATER, W. L. . . — The Mammals of South Africa.
The Fauna of South Africa, ed. by W. L. Sclater. 2 vols. London. 1900–1901.

TROUESSART, E. L. . — Catalogus Mammalium tam Viventium quam Fossilium. 5th ed. Berlin. 1904–1905. [Key to the literature of recent and fossil species.]

WEBER, M. . . . . — Die Säugetiere. Jena. 1904. [The leading text-book on mammals. Especially good on anatomy and classification.]

ZITTEL, K. A. VON . — Handbuch der Paläontologie. Vol. IV, Vertebrata (Mammalia). Munich. 1891–1893. [Numerous figures, especially of European fossils.]

Class MAMMALIA, Mammals

A. Subclass PROTOTHERIA. Egg-laying Mammals.

I. Order **PROTODONTA.**[1] Protodonts (doubtfully placed here).

† *Dromatherium.*[1] U. Trias., N. Amer.

† *Microconodon.*[1] U. Trias., N. Amer.

Inc. Sed. † *Karoomys.* U. Trias., S. Afr. (Possibly a theriodont reptile.)

II. Order **MONOTREMATA.** Monotremes.

Fam. '**Echidnidæ**' (= Tachyglossidæ). Spiny Anteaters.

'*Echidna*' (= Tachyglossus). Echidna. Austral.

'*Proëchidna*' (= *Zaglossus*). Long-snouted Echidna. New Guin.

Fam. **Ornithorhynchidæ.** Duckbills.

Ornithorhynchus. Duckbill or Platypus. Austral.

B. Subclass EUTHERIA.[2] Viviparous Mammals.

AA. Infraclass DIDELPHIA (Metatheria). Marsupials.

I. Order **TRICONODONTA.**[3] Triconodonts or Mesozoic Carnivorous Marsupials (?).

† *Amphilestes.* M. Jur., England.

† *Phascolotherium.* M. Jur., England.

† *Triconodon.* M. & U. Jur., England & N. Amer.

† *Spalacotherium.* U. Jur., England.

II. Order **MARSUPIALIA.**[4] Marsupials or Pouched Mammals.

II. 1. Suborder **Polyprotodontia.** Chiefly Insectivorous and Carnivorous Marsupials and their Allies.

Inc. Sed. † *Pediomys.* U. Cret., N. Amer.

Inc. Sed. † *Didelphops.* U. Cret., N. Amer.

Inc. Sed. † *Caroloameghinia.* Eoc., S. Amer.

Superfam. *Didelphoidea.* Didelphoids.

Fam. **Didelphiidæ.** Opossums.

† *Proteodidelphys.* L. Eoc., S. Amer.

[1] *Vide* Osborn, Evolution of Mammalian Molar Teeth, 1907, pp. 18–21.

[2] Gill in 1871 used this term to embrace both Marsupialia and Placentalia. Huxley used it to designate the hypothetical ancestors of the Placentals. Gill's usage is here followed.

[3] See Osborn, Evolution of Mammalian Molar Teeth, 1907, pp. 21–30, figs. A–35.

[4] For a general review of the inter-relationships of the marsupial families, see Bensley, B. A., On the Evolution of the Australian Marsupials, with Remarks on the Relationships of the Marsupials in General. *Trans. Linn. Soc., London,* ser. 2, Zoöl. Vol. IX, Pt. 3, Dec., 1903, pp. 83–217; and Gregory, W. K., The Orders of Mammals, *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVII, 1910, pp. 1–524. The present arrangement by Gregory embodies the chief results of many earlier authors (especially de Blainville, Owen) and of Dollo, Bensley, Ameghino, Sinclair, and others.

† *Peratherium.* L. Eoc. to M. Olig., N. Amer.; U. Eoc. to L. Mioc., Eur.

† *Amphiperatherium.* L. to U. Olig., Eur.

† *Microbiotherium.* U. Mioc., S. Amer.

Marmosa. Murine Opossum. Brazil to Mex.

Chironectes. Water Opossum. Brazil to Panama.

'*Philander*' (= *Caluromys*). Woolly Opossum. C. & S. Amer.

Didelphis. Opossum. Brazil to mid. U. S. (Pleist., S. Amer.).

FAM. **Myrmecobiidæ.** Banded Anteaters.

Myrmecobius. Banded Anteater. Austral.

FAM. **Dasyuridæ.** Pouched Mice, Dasyures, etc.

SUBFAM. Phascologalinæ. Phascologales, etc.

Phascologale. Phascologale. Austral., New Guin.

Sminthopsis. Pouched Mouse. Austral.

Antechinomys. Jerboa Pouched Mouse. Austral.

SUBFAM. Dasyurinæ. Dasyures, etc.

Dasyurus. Dasyure or 'Native Cat.' Austral., New Guin. (Pleist., Austral.).

Sarcophilus. Tasmanian Devil. Tasman. (Pleist., Austral.).

FAM. **Thylacynidæ.** Thylacines and Sparassodonts.

SUBFAM. Thylacininæ. Australian and Tasmanian Thylacines.

Thylacynus. Tasmanian 'Wolf.' Tasman. (Pleist., Austral.).

SUBFAM. Borhyæninæ. Extinct South American Thylacines.[1]

† *Pharsophorus.* U. Eoc., S. Amer.

† *Amphiproviverra.* U. Mioc., S. Amer.

† *Cladosictis.* U. Mioc., S. Amer.

† *Prothylacynus.* U. Mioc., S. Amer.

† *Borhyæna.* U. Mioc., S. Amer.

SUPERFAM. *PERAMELOIDEA.* Perameloids.

FAM. **Peramelidæ.** Bandicoots.

Perameles. True Bandicoot. Austral., New Guin. (Pleist., Austral.).

Chœropus. Pig-footed Bandicoot. Austral.

Thylacomys. Rabbit Bandicoot. Austral.

SUPERFAM. *NOTORYCTOIDEA.* Notoryctoids.

FAM. **Notoryctidæ.** Pouched Moles.

Notoryctes. Pouched Mole. Austral.

[1] Sinclair, W. J., Marsupialia of the Santa Cruz Beds. Rep'ts Princeton Univ. Exped. Patagonia, 1896–1899. Palæont., Vol. IV, Pt. III, 1906, pp. 333–460.

II. 2. Suborder **Diprotodontia**. Mostly Herbivorous Marsupials.

Superfam. *Cænolestoidea*. Cænolestoids.

Fam. '**Epanorthidæ** (=Palæothentidæ). Epanorthids.[1]

† '*Epanorthus*' (=*Palæothentes*). U. Mioc., S. Amer.

† *Abderites*. U. Mioc., S. Amer.

Cænolestes. Cænolestes. C. Amer., Colombia.

Fam. **Garzoniidæ**. Garzoniids.

† *Garzonia*. U. Mioc., S. Amer.

† *Stilotherium*. U. Mioc., S. Amer.

Superfam. *Phalangeroidea*. Phalangeroids.

Fam. **Phalangeridæ**. Phalangers.

Subfam. Tarsipedinæ. Tarsipedes.

Tarsipes. Long-snouted Phalanger. Austral.

Subfam. Phalangerinæ. Phalangers.

Acrobates. Pigmy Flying Phalanger. Austral.

Distæchurus. Pen-tailed Phalanger. New Guin.

Dromicia. Dormouse Phalanger. Austral., New Guin.

Gymnobelideus. Leadbeater's Phalanger. Austral.

Petaurus. True Flying Phalanger. Austral., New Guin.

Dactylopsila. Striped Phalanger. New Guin., Austral.

Petauroides. Taguan Flying Phalanger. Austral.

Trichosurus. True Phalanger. Austral.

Phalanger. Cuscus. Austral., New Guin., Moluccas, Celebes.

Subfam. Phascolarctinæ, Koalas, etc.

Pseudochirus. Crescent-toothed Phalanger. Austral., New Guin. (Pleist., Austr.).

Phascolarctos. Koala or 'Marsupial Bear.' Austral.

Fam. **Thylacoleonidæ**. Thylacoleos.

† *Thylacoleo*. 'Marsupial Lion.' Pleist., Austral.

Fam. **Macropodidæ**. Kangaroos, etc.

Subfam. Bettongiinæ. Musk Kangaroos, etc.

Æpyprymnus. Rufous Rat-Kangaroo. Austral. (from Pleist.).

Bettongia. Brush-tailed Rat-Kangaroo. Austral. (from Pleist.).

Potoröus. Common Rat-Kangaroo. Austral.

Hypsiprymnodon. Five-toed or Musk Kangaroo. Austral.

[1] *Vide* Sinclair, *op. cit.*, *supra*.

SUBFAM. Macropodinæ. Kangaroos and Wallabies.

Dorcopsis. Müller's Kangaroo. New Guin.

Dendrolagus. Tree Kangaroo. New Guin., Austral.

Lagorchestes. Hare Wallaby. Austral.

Onychogale. Spur-tailed Wallaby. Austral.

Petrogale. Rock Wallaby. Austral.

Macropus. Kangaroo & Wallaby. Austral., New Guin. (Pleist., Austral).

† *Palorchestes.* Pleist., Austral.

† *Sthenurus.* Pleist., Austral.

FAM. **Phascolomyidæ.** Wombats.

Phascolomys. Wombat. Austral. (from Pleist.).

† *Phascolonus.* Pleist., Austral.

FAM. **Diprotodontidæ.** Giant, Ground-sloth Marsupials.

† *Nototherium.* Nototherе. Pleist., Austral.

† *Diprotodon.* Giant Diprotodon. Pleist., Austral.

II. 3. SUBORDER '**MULTITUBERCULATA**' (=Allotheria). Multituberculates, Archaic Diprotodont Marsupials.[1]

Inc. Sed. † *Tritylodon.* (?) L. Jur., S. Afr.

FAM. **Plagiaulacidæ.** Plagiaulacids.

† *Microlestes.* U. Trias., Eur.

† *Triglyphus.* U. Trias., Germany.

† *Plagiaulax.* U. Jur., Eur. & N. Amer.

† *Bolodon.* U. Jur., N. Amer.

† *Allodon.* U. Jur., N. Amer.

† *Ctenacodon.* U. Jur., Eur. & N. Amer.

† *Ptilodus* (incl. *Chirox*). U. Cret. & Bas. Eoc., N. Amer.

† *Neoplagiaulax.* Bas. Eoc., Eur. & N. Amer.

† *Meniscoëssus.* U. Cret., N. Amer.

† *Polymastodon.* Bas. Eoc., N. Amer.

BB. INFRACLASS MONODELPHIA. Placentals.

a. COHORT UNGUICULATA. Clawed Mammals.

[1] *Vide* Osborn, H F., The Structure and Classification of the Mesozoic Mammalia. *Journ. Acad. Nat. Sci.*, Phila., Vol. IX, 1888, pp. 186–265.

For a brief review see Osborn, H. F., Evolution of Mammalian Molar Teeth, 1907, pp. 101–106. Gidley has recently shown that the skull of *Ptilodus* is of the marsupial type.

A number of extinct Patagonian forms (e.g. *Propolymastodon*, *Polydolops*) which are referred to this order by Ameghino may possibly prove to represent highly specialized Cænolestoids. (W. K. G.)

I. Order '**TRITUBERCULATA**' in part (= Pantotheria). Trituberculates or Mesozoic Insectivores.[1]

Fam. **Amphitheriidæ**. Amphitheres.

† *Amphitherium*. Jur., England, N. Amer.

Fam. **Amblotheriidæ**. Amblotheres.

† *Dryolestes*. Jur., N. Amer., England.

† *Amblotherium*. U. Jur., England.

II. Order **INSECTIVORA**.[2] Insectivores.

1. Suborder **Lipotyphla**. Insectivores with pubic symphysis typically short or absent. Cæcum absent.

Inc. Sed. Fam. **Pantolestidæ**. Pantolestids. Eocene aquatic Insectivores, with creodont-like teeth.

† *Pentacodon*. Bas. Eoc., N. Amer.

† *Palæosinopa*. L. Eoc., N. Amer.

† '*Pantolestes*' (= *Anisacodon*, *Passalacodon*). M. Eoc., N. Amer.

1. Section *ZALAMBDODONTA*. Zalambdodonts. Molar cusps forming a single V.

Superfam. *Centetoidea*. Centetoids.

Fam. **Apternodontidæ**, Matthew. Apternodonts. North American Oligocene Centetoids.

† *Apternodus*. L. Olig., N. Amer.

Fam. **Centetidæ**. Madagascan Tenrecs, etc.

Subfam. Oryzorictinæ.

Microgale. Long-tailed Tenrec. Madag.

Oryzorictes. Rice Tenrec. Madag.

Limnogale. Limnogale. Madag.

Geogale. Geogale. Madag.

[1] *Vide* Osborn, H. F., Evolution Mammalian Molar Teeth, 1907, pp. 21–30, figs. 12–35; Gidley, J. W., Evidence Bearing on Tooth-cusp Development. *Proc. Wash. Acad. Sci.*, Vol. VIII, 1906, pl. V (teeth of Mesozoic mammals).

[2] See especially the following authors:

Dobson, G. E. A Monograph on the Insectivora. London. 1882–1883.

Gill, T. Synopsis of Insectivorous Mammals. *Bull. U.S. Geol. and Geogr. Surv. Terr.*, No. 2, 1875, pp. 91–120.

Gregory, W. K. The Orders of Mammals. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVII, 1910, pp. 231–287.

Leche, W. Zur Entwicklungsgeschichte des Zahnsystems der Säugetiere. *Chun's Zoölogica*. Stuttgart, 1895–1907.

Matthew, W. D. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. *Mem. Amer. Mus. Nat. Hist.*, Vol. IX, pt. vi, 1909.

Mivart, St. George. Notes on the Osteology of the Insectivora. *Journ. Anat. and Physiol.*, Vol. I, 1867, pp. 281–312; Vol. II, 1868, pp. 117–154.

The present arrangement is by Matthew and Gregory.

SUBFAM. Centetinæ.

Ericulus. Hedgehog Tenrec. Madag.

Centetes. Common Tenrec. Madag.

Hemicentetes. Streaked Tenrec. Madag.

SUBFAM. Potamogalinæ. West African Aquatic Centetoids.

Potamogale. Potamogale. W. Afr.

FAM. **Solenodontidæ**. Solenodonts.

Solenodon. Alamiqui. Cuba, Haiti.

† *Micropternodus*. L. Olig., N. Amer.

SUPERFAM. *CHRYSOCHLOROIDEA*. Chrysochloroids.

Inc. Sed. Chrysochloroidea.

† *Xenotherium*. L. Olig., N. Amer.

† *Arctoryctes*. L. Mioc., N. Amer.

FAM. **Chrysochloridæ**. Golden Moles or Chrysochlorids and their Allies.

Chrysochloris. Cape Golden Mole. S. Afr.

FAM. **Necrolestidæ**. Necrolestids. Patagonian Chrysochloroids.

† *Necrolestes*. U. Mioc., S. Amer.

2. SECTION *ERINACEOMORPHA*. Ancient and Modernized Hedgehogs.

SUPERFAM. *ERINACEOIDEA*. Erinaceoids.

FAM. **Leptictidæ**. Primitively Trituberculate Erinaceoids.

† *Palæictops*. L. Eoc., N. Amer.

† *Parictops*. L. Eoc., N. Amer.

† *Ictops*. L. to M. Olig., N. Amer.

† *Leptictis*. M. Olig., N. Amer.

† *Mesodectes*. M. Olig., N. Amer.

FAM. **Erinaceidæ**. Hedgehogs, Quadrituberculate Erinaceoids.

† *Tetracus*. L. Olig., Eur.

† *Proterix*. M. Olig., N. Amer.

† *Palæoerinaceus*. U. Olig., Eur.

† *Neurogymnurus*. U. Eoc. to L. Olig., Eur.

† *Galerix*. M. Mioc., Eur.

† *Lanthanotherium*. M. Mioc., Eur.

Hylomys. Lesser Gymnura. E. Indies, Burma.

Gymnura. Bulau or Gymnura. E. Indies, Burma.

Erinaceus. Hedgehog. Eur., Asia, N. Afr. (L. Mioc. to Pleist., Eur.).

Inc. Sed. Fam. **Dimylidæ**. Dimylids.

† *Dimylus*. U. Olig. to U. Mioc., Eur.

† *Cordylodon*. U. Olig., Eur.

† *Plesiodimylus*. M. Mioc., Eur.

3. Section *SORICOMORPHA*. Shrews, Shrew Moles, and Moles.

Superfam. *Soricoidea*. Soricoids.

Soricoidea Fam. *Incert.*

† *Nyctitherium* (*Talpavus*, *Nyctilestes*). M. Eoc., N. Amer.

Fam. **Talpidæ**. Moles and Shrew Moles.

Subfam. Myogalinæ. Desmans.

† *Georhynchus*. M. Olig., Colorado.

† *Domnina*. M. Olig., Colorado.

† *Proscalops*. U. Olig., N. Amer.

Uropsilus. Thibetan Shrew Mole. Thibet, China.

Urotrichus. Shrew Mole. Japan.

Neürotrichus. Shrew Mole. N. Amer.

Myogale. Desman. Eur.

Subfam. Talpinæ. Moles.

† *Amphidozotherium*. U. Eoc., Eur.

† *Geotrypus*. M. Olig., Eur.

Talpa. European Mole, from U. Olig., Eur.; M. Mioc., N. Amer.

† *Proscapanus*. M. Mioc., Eur.

† *Scaptonyx*. M. Mioc., Eur.

Scalops. American Web-footed Mole. U.S.A. (from Pleist.).

Scapanus. Hairy-tailed Mole. West N. Amer.

Condylura. Star-nosed Mole. N. Amer.

Fam. **Soricidæ**. Shrews.

Subfam. Soricinæ. Red-toothed Shrews.

† *Amphisorex*. M. Olig., Eur.

Sorex. Shrew. Eur., As., N. Amer. (M. Olig. to Pleist., Eur.; Pleist., N. Amer.).

† *Protosorex*. Olig., N. Amer.

Soriculus. Oriental Shrew. India, China.

Blarina. Short-tailed Shrew. N. Amer. (from Pleist.).

Crossopus. Water Shrew. Eur., As. (from Pleist.).

Subfam. Crocidurinæ. White-toothed Shrews.

Crocidura. Musk Shrew. As., Afr. (M. Mioc. to Pleist., Eur.).

Myosorex. Mouse Shrew. S. Afr.

Anurosorex. Burrowing Shrew. Thibet, Burma.

Nectogale. Web-footed Shrew. Thibet, China.

Chimarrogale. Mountain Shrew. As., E. Indies.

2. Suborder **Hyopsodonta** *div. nov.*[1] Hyopsodonts.

Fam. **Hyopsodontidæ.** Hyopsodonts.

† *Hyopsodus.* L. to U. Eoc., N. Amer.

3. Suborder **Proglires.** Proglires, Diprotodont or Rodent-like Insectivores.

Fam. **Apatemyidæ.** Apatemyids.

† *Apatemys.* M. Eoc., N. Amer.

† *Uintasorex.* M. Eoc., N. Amer.

† *Trogolemur.* M. Eoc., N. Amer.

Fam. **Mixodectidæ.** Mixodectids.

† *Mixodectes.* Bas. Eoc., N. Amer.

† *Olbodotes.* Bas. Eoc., N. Amer.

† *Indrodon.* Bas. Eoc., N. Amer.

† *Cynodontomys.* L. Eoc., N. Amer.

† *Microsyops.* M. Eoc., N. Amer.

Subord. Inc. Fam. **Adapisoricidæ.** Adapisoricids, Primitive Tupaia-like Insectivores.

† *Adapisorex.* L. Eoc., Eur.

† *Adapisoriculus.* L. Eoc., Eur.

4. Suborder **Menotyphla.** Menotyphla.

Fam. **Tupaiidæ.** Oriental Tree Shrews.

Tupaia. Tupai or Tree Shrew. India, E. Indies.

Ptilocercus. Pen-tailed Tree Shrew. Borneo.

† ? *Entomolestes.* M. Eoc., N. Amer.

Fam. **Macroscelididæ.** African Jumping Shrews.

Macroscelides. Elephant Shrew. Afr.

Petrodromus. Four-toed Elephant Shrew. Afr.

Rhynchocyon. Long-nosed Jumping Shrew. Afr.

Subord. Inc. † *Plesiosorex.* M. Olig., Eur.

[1] Characters given in Matthew, The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. *Mem. Amer. Mus. Nat. Hist.*, Vol. IX, pt. vi, 1909, pp. 507–513.

III. Order **TILLODONTIA**. Tillodonts or Archaic Diprotodont Placentals.[1]

Fam. **Esthonychidæ** or **Anchippodontidæ** (=Tillotheriidæ). Anchippodonts.

† (?) *Anchippodus*. Mioc. (?), N.J.

† *Esthonyx*. L. Eoc., N. Amer.

† *Trogosus*. M. Eoc., N. Amer.

† *Tillotherium*. M. Eoc., N. Amer.

IV. Order **DERMOPTERA**. Dermoptera.[2]

Fam. **Galeopithecidæ**. Colugos.

Galeopithecus. Colugo, Flying "Lemur." Burma to Borneo, Philippines.

V. Order **CHIROPTERA**. Bats.[3]

1. Suborder '**Megachiroptera**' (= Frugivora). Fruit-eating Bats.

Fam. **Pteropidæ**. Fruit Bats.

Subfam. Pteropinæ. Common Fruit Bats.

Epomophorus. Epauleted Fruit Bat. Afr.

Pteropus. Flying Fox. S.E. As., E. Indies, Austral.

Pteralopex. Cusped-toothed Fruit Bat. E. Indies.

'*Cynonicteris*' (= *Rousettus*). Dog Bat. Afr., S. As., E. Indies, (M. Mioc., Eur.).

'*Harpyia*' (= *Nyctymene*). Tube-nosed Fruit Bat. E. Indies, Austral.

Cynopterus. Short-nosed Fruit Bat. India, Indo-China, E. Indies.

Subfam. 'Macroglossinæ' (= Kiodontinæ). Long-tongued Fruit Bats.

'*Macroglossus*' (= *Kiodon*). Long-tongued Fruit Bat. Indo-China, E. Indies, Austral.

Subfam. Harpyionycterinæ. Harpy Bats.

Harpyionycteris. Harpy Bat. Philippine Islands.

2. Suborder '**Microchiroptera**' (= Animalivora). Insect-eating Bats.

[1] *Vide* Marsh, O. C., Principal Characters of the Tillodontia. *Amer. Jour. Sci.* (3), XI, 1876, pp. 249–252, Pl. VIII, IX. For reasons for regarding the tillodonts as an offshoot of the insectivore-creodont stock not related to the rodents, see Gregory, W. K., The Orders of Mammals. *Bull. Amer. Mus. Nat. Hist.*, Vol. XXVII, 1910, pp. 292–294.

[2] *Vide* Weber, Die Säugetiere, pp. 406–410.

[3] *Vide* Weber, Die Säugetiere, pp. 382–406; Elliot, D. G., The Land and Sea Mammals of Middle America and the West Indies, Pt. II, pp. 569–722; Miller, G. S., The Families and Genera of Bats. *Smithsonian Institution, U.S. Nat. Mus.*, Bull. 57, 1907.

The present arrangement by Gregory is adapted chiefly from Miller, and aims to give only the better known genera and subfamilies.

FAM. **Emballonuridæ**. Large-eared Bats.

SUBFAM. Rhinopominæ. Long-tailed Bats.

Rhinopoma. Long-tailed Bat. N. Afr., S. As.

SUBFAM. Emballonurinæ. Sheath-tailed Bat, Tomb Bat, etc.

Emballonura. Sheath-tailed Bat. Madag., Indo-China, E. Indies, Polynesia.

Taphozous. Tomb Bat. Afr., S. As., E. Indies, Austral.

Saccopteryx. Pouch-winged Bat. S. Amer., C. Amer., Mexi.

SUBFAM. Diclidurinæ. White Bats.

Diclidurus. White Bat. C. Amer., S. Amer.

FAM. **Rhinolophidæ**. Noseleaf Bats.

SUBFAM. Megaderminæ. Hispid Bat, False Vampire, etc.

Nycteris. Hispid Bat. Afr., E. Indies.

Megaderma. False Vampire. Afr., India, E. Indies, Austral.

SUBFAM. Rhinolophinæ. Cyclops, Horseshoe Bat, etc.

† *Pseudorhinolophus*. U. Eoc., Eur.

Rhinolophus. Horseshoe Bat. Eur. (since M. Mioc.), As., E. Indies, Austral., Afr.

SUBFAM. Hipposiderinæ.

'*Phyllorhina*' (= *Hipposiderus*). Leaf-nosed Bat, Cyclops Bat. Afr., S. As. (since Pleist.), E. Indies, Austral.

FAM. **Noctilionidæ**. Hare-lipped Bats.

Noctilio. Hare-lipped Bat. S. Amer.

FAM. **Phyllostomidæ**. Vampire Bats.

SUBFAM. 'Lobostominæ' (= Chilonycterinæ). Cinnamon Bat Hare-lipped Bat, etc.

'*Lobostoma*' (= *Chilonycteris*). Chin-leafed Bat. W. Indies, Mexi. to Brazil.

Mormoöps. Cinnamon Bat. W. Indies, Mexi., C. Amer., S. Amer.

SUBFAM. Phyllostominæ. American Leaf-nosed Bats.

Otopterus. California Leaf-nosed Bat. W. Indies, Cal., Mexi.

Lonchorhina. Tome's Long-eared Bat. W. Indies.

Vampyrus. Vampire. C. Amer. to Brazil (since Pleist.).

Phyllostomus. Javelin Bat. S. Amer. (since Pleist.).

SUBFAM. Glossophaginæ. Long-tongued Vampire, etc.

Glossophaga. Long-tongued Vampire. Mexi. to Brazil, Chili.

Chœronycteris. Tres Marias Islands Bat. Mid. Am.

SUBFAM. Phyllonycterinæ. Poey's Bat, etc.

Phyllonycteris. Poey's Bat. W. Indies.

SUBFAM. Stenoderminæ. Centurion Bat, Short-nosed Vampire, etc.

Brachyphylla. Cavern Nose-leaf Bat. W. Indies.

Artibeus. Short-nosed Vampire. Florida, Mexi., C. Amer., S. Amer.

Stenoderma. Cinereous Bat. W. Indies, Brazil.

Centurio. Centurion Bat. Mexi., C. Amer., Cuba.

Vampyrops. White-striped Bat. Mexi., C. Amer., S. Amer. (since Pleist.).

SUBFAM. Desmodontinæ. Blood Vampires.

Desmodus. Common Blood-sucking Vampire. Mexi. to Paraguay (since Pleist.).

Diphylla. Smaller Blood-sucking Vampire. Mexi. to Brazil.

FAM. **Natalidæ.** Funnel-eared Bats.

SUBFAM. Natalinæ. Tall-crowned Bat, etc.

Natalus. Tall-crowned Bat. N. Amer.

Nyctiellus. Graceful Bat. Cuba.

SUBFAM. Furipterinæ. Fury.

'*Furia*' (= *Furipterus*). Fury. S. Amer.

SUBFAM. Thyropterinæ. American Sucker-footed Bats.

Thyroptera. Tricolor Bat. Tropical Amer.

SUBFAM. Myzopodidæ. Madagascan Sucker-footed Bats.

Myzopoda. Golden Bat. Madag.

FAM. **Vespertilionidæ.** Simple-faced Bats.

SUBFAM. Vespertilioninæ. Common Bats.

† *Vespertiliavus.* U. Eoc., Eur.

† *Palæonycteris.* L. Olig., Eur.

Vespertilio. Brown Bat, etc. Asia, Eur. (since M. Mioc.); N. and S. Amer. (since Pleist.); Afr., Austral.

'*Vesperugo*' (= *Pipistrellus*). Pipistrelle, Noctule, etc. As., Eur. (since M. Mioc.); N. Amer., S. Amer., Afr., Austral.

Myotis. Pale Bat, Large-winged Bat, Small-winged Bat. As., Eur., N. Amer. (since Pleist.); S. Amer., Afr., Austral.

'*Atalapha*' (= *Lasiurus*). Hoary Bat, Red Bat. N. Amer., S. Amer., W. Indies.

Nycticejus. White-winged Bat. U.S.A., C. Amer., W. Indies.

Rhogeëssa. Restless Bat. Mid. Amer.

Kerivoula. Indian Painted Bat. Afr., India, E. Indies.

SUBFAM. Plecotinæ. Big-eared Bats.

Plecotus. Big-eared Bat. Eur., Asia, N. Afr., U.S.A., Mexi.

'*Synotus*' (= *Barbastella*). Barbastelle. As., Eur., N. Afr.

Otonycteris. Hemprich's Eared Bat. N. Afr., S.W. As.

SUBFAM. Nyctophilinæ. Horseshoe-nosed Bats.

Nyctophilus. Australian Big-eared Bat. Austral., N. Guin.

Antrozoüs. Californian Cave Bat. W. U.S.A., Mexi.

SUBFAM. Miniopterinæ. Long-winged Bats.

Miniopterus. Long-winged Bat. As., Eur., Afr., Austral., E. Indies.

SUBFAM. Murininæ. Tube-nosed Bats.

Murina. Murina. Malay region, S. and E. As.

Harpiocephalus. Tube-nosed Bat. Malay Region, India.

SUBFAM. Tomopeatinæ.[1]

Tomopeas. Tomopeas. Peru.

SUBFAM. Mystacopinæ. New Zealand Bat.

Mystacops. New Zealand Bat. New Zealand.

SUBFAM. Molossinæ. Mastiff Bat, Naked Bat, etc.

Molossus. Mastiff Bat. Mexi., C. Amer., S. Amer.

Promops. Bonneted Bat. W. U.S.A., C. Amer., S. Amer.

Nyctinomus. Free-tailed Bat. Afr., Eur., As., N., C., S. Amer., Austral.

Chiromeles. Naked Bat. E. Indies.

VI. ORDER **CARNIVORA**. Carnivores.

1. SUBORDER **CREODONTA**. Creodonts or Archaic Carnivores.[2]

Inc. Sed.

FAM. **Oxyclænidæ**. Oxyclænids or Tritubercular Creodonts.

† *Oxyclænus.* Bas. Eoc., N. Amer.

† *Chriacus.* Bas. Eoc., N. Amer.

† *Tricentes.* Bas. Eoc., N. Amer.

† *Deltatherium.* Bas. Eoc., N. Amer.

FAM. **Arctocyonidæ**. Arctocyonids or Omnivorous Bear-like Creodonts (with affinities to Eucreodi).

† *Arctocyon.* Bas. Eoc., Eur.

[1] Peruvian Bats connecting the Molossinæ with the more primitive Vespertilioninæ (Miller, 1907, p. 237).

[2] *Vide* Matthew, W. D., The Carnivora and Insectivora of the Bridger Basin, Middle Eocene, *op. cit, supra.* The present arrangement is chiefly by Matthew.

† *Clænodon.* Bas. Eoc., N. Amer.

† *Anacodon.* L. Eoc, N. Amer.

(1) Section *ACREODI* (without carnassial teeth).

Superfam. *MESONYCHOIDEA.* Mesonychoids.

Fam. **Mesonychidæ.** Mesonychids and Triisodonts.

† *Triisodon.* Bas. Eoc., N. Amer.

† *Sarcothraustes.* Bas. Eoc., N. Amer.

† *Goniacodon.* Bas. Eoc., N. Amer.

† *Dissacus.* Bas. Eoc., N. Amer.

† *Hyænodictis.* Bas. Eoc., Eur.

† *Pachyæna.* L. Eoc., N. Amer. & Eur.

† *Mesonyx.* M. Eoc., N. Amer.

† *Synoplotherium* (incl. *Dromocyon*). M. Eoc., N. Amer.

† *Harpagolestes.* M. to U. Eoc., N. Amer.

† *Hapalodectes.* L. Eoc., N. Amer.

(2) Section *PSEUDOCREODI* (with aberrant carnassial teeth).

Superfam. *OXYÆNOIDEA.* Oxyænoids.

Fam. **Oxyænidæ.** Oxyænids and Palæonictids.

† *Palæonictis.* L. Eoc., N. Amer. & Eur.

† *Ambloctonus.* L. Eoc., N. Amer.

† *Oxyæna.* L. Eoc., N. Amer.

† *Patriofelis.* M. Eoc., N. Amer.

† *Limnocyon.* M. to U. Eoc., N. Amer.

† *Thinocyon.* M. Eoc., N. Amer.

† *Oxyænodon.* U. Eoc., N. Amer.

Fam. **Hyænodontidæ.** Hyænodonts.

† *Proviverra.* M. Eoc., Eur.

† *Sinopa.* L. to M. Eoc., N. Amer.; M. Eoc., Eur.

† *Tritemnodon.* M. Eoc., N. Amer.

† *Cynohyænodon.* U. Eoc., Eur.

† *Galethylax.* U. Eoc., Eur.

† *Quercytherium.* U. Eoc. to L. Olig., Eur.

† *Apterodon.* U. Eoc. to L. Olig., Eur.; L. Olig., N. Afr.

† *Pterodon.* U. Eoc. to L. Olig., Eur.; L. Olig., N. Afr.

† *Metasinopa.* L. Olig., N. Afr.

† *Hemipsalodon.* L. Olig., N. Amer.

† *Hyænodon.* L. to M. Olig., N. Amer. & Eur.

(3) Section *EUCREODI* (with typical carnassial teeth).

Fam. **Miacidæ**. Miacids or Primitive Dog-like Carnivores.

Viverroid or Civet-like (with cutting teeth).

† *Didymictis*. Bas. to L. Eoc., N. Amer.

† *Viverravus*. L. to M. Eoc., N. Amer.

Cynoid or Dog-like.

† *Miacis*. L. to U. Eoc., N. Amer.

† *Uintacyon*. L. to M. Eoc., N. Amer.

Procyonoid or Raccoon-like.

† *Oödectes*. L. to M. Eoc., N. Amer.

† *Vulpavus*. L. to M. Eoc., N. Amer.

† *Palæarctonyx*. M. Eoc., N. Amer.

2. Suborder **Fissipedia**. Modernized, chiefly Terrestrial Carnivora.[1]

(1) Section *ARCTOIDEA*. Dogs, Raccoons, Bears, Mustelines.

Fam. **Canidæ**. Dogs, Wolves, Foxes, etc.

Typical Group.

† *Procynodictis*. U. Eoc., N. Amer.

† *Cynodictis*. U. Eoc. to L. Olig., Eur.; L. to U. Olig., N. Amer.

† *Cynodon*. U. Eoc. to U. Olig., Eur.; L. Olig., N. Amer.

† *Amphicynodon*. L. Olig., Eur.

† *Cephalogale*. U. Olig., Eur.

† *Cynodesmus*. L. Mioc., N. Amer.

† *Nothocyon*. U. Olig., N. Amer.

† *Galecynus*. U. Mioc., Eur.

† *Mesocyon*. U. Olig., N. Amer.

† *Tephrocyon*. M. Mioc. to L. Plioc., N. Amer.

† *Ælurodon*. U. Mioc. to L. Plioc., N. Amer.

Canis. Dog, Jackal, Wolf. N. Amer., S. Amer., Eur., As., Afr., Austral. (Since L. Plioc. in As.; U. Plioc. in Eur.; elsewhere since Pleist.)

Vulpes. Red Fox. Eur., Afr., As., N. Amer. (Since U. Plioc. in As.; Pleist. in Eur.)

Urocyon. Gray Fox. U.S.A., Mexi. to Colombia. (N. Amer. since Pleist.)

Otocyon. Large-eared Dog. E. & S. Afr.

[1] For the general classification see Flower and Lydekker, Introduction to the Study of Mammals, 1891; Weber, Die Säugetiere, 1904 (pp. 529-538). The present arrangement is by Matthew and Osborn.

Cyon or Dhole-like Group.

† *Daphænus.* L. to M. Olig., N. Amer.

† *Temnocyon.* U. Olig., N. Amer.

† *Simocyon.* U. Mioc. to L. Plioc., Eur.

† *Enhydrocyon.* U. Olig., N. Amer.

† *Dinocynops.* Pleist., S. Amer.

Icticyon. South American Bush Dog. Guiana, Brazil (since Pleist.).

Cyon. Dhole, Buansuah, etc. As., E. Indies (? M. to U. Mioc., N. Amer.).

Lycaon. Cape Hunting Dog. Afr. (Pleist., Eur.).

Amphicyon Group (Bear-like Dogs).

† *Daphænodon.* U. Olig., N. Amer.

† *Amphicyon.* U. Olig. to M. Mioc., Eur.; M. Mioc. to L. Plioc., N. Amer.

† *Pseudocyon.* M. Mioc., Eur.

† *Hemicyon.* M. Mioc., Eur.

† *Ischyrocyon.* U. Mioc., N. Amer.

† *Dinocyon.* U. Mioc. to Plioc., Eur.

† *Borophagus.* U. Mioc. to M. Plioc., N. Amer.

Fam. **Procyonidæ.** Raccoons.

Subfam. Cercoleptinæ. Kinkajous.

'*Cercoleptes*' (= *Potos*). Kinkajou. N. S. Amer. to Mexi.

Subfam. Procyoninæ. Raccoons, Coatis.

Bassaricyon. Bassaricyon. C. Amer. to Ecuador.

Bassariscus. Cacomistle. W. U.S.A., Mexi., C. Amer. (L. Plioc., N. Amer.).

† *Phlaocyon.* Primitive Raccoon. L. Mioc., N. Amer.

† *Leptarctus.* Primitive Raccoon. U. Mioc., N. Amer.

Procyon. Raccoon. S. Canada to Paraguay (Pleist., N. Amer.).

† *Cyonasua.* Plioc., S. Amer.

Nasua. Coati. S. Amer. to California.

Subfam. Ælurinæ. Pandas.

Ælurus. Panda. Himalayas to Assam (Plioc., Eur.).

Æluropus. Particolored Bear. C. As.

Fam. **Ursidæ.** Bears.

† (?) *Ursavus.* M. Mioc., Eur.

† (?) *Hyænarctos.* L. Plioc., Eur. & As.

† *Pseudarctos.* M. Mioc., Eur.

Ursus. Grizzly Bear, Black Bear, Brown Bear, etc. N. Amer. (since Pleist.); As. (since L. Plioc.); Eur. (since U. Plioc.); N. Afr.

Thalarctos. Polar Bear. Arctic Reg. of the World.

Tremarctos. Spectacled Bear. W. S. Amer. (Andes Mts.).

† *Arctotherium.* Pleist., N. Amer. & S. Amer.

† *Pararctotherium.* Pleist., S. Amer.

Melursus. Sloth Bear. India.

FAM. **Mustelidæ.** Mustelines.

SUBFAM. Mustelinæ. Martens, Weasels, Wolverines.

† *Proplesictis.* L. Olig., Eur.

† *Plesictis.* U. Eoc. to L. Mioc., Eur.

† *Amphictis.* L. to U. Olig., Eur.

† *Palæogale.* U. Eoc. to L. Mioc., Eur.

† *Stenogale.* L. Olig. to L. Mioc., Eur.

† *Bunælurus.* L. to M. Olig., N. Amer.

† *Oligobunis.* U. Olig. to L. Mioc., N. Amer.

† *Proælurus.* U. Olig., Eur.

† *Stenoplesictis.* L. Olig., Eur.

† *Ælurocyon.* L. Mioc., N. Amer.

† *Megalictis.* L. Mioc., N. Amer.

† *Haplogale.* L. Olig. to U. Mioc., Eur.

† *Proputorius.* M. Mioc., Eur.

† *Brachypsalis.* U. Mioc., N. Amer.

Mustela. Marten. N. Amer., Eur., As., E. Indies (since M. Mioc., Eur., As., N. Amer.).

† *Canimartes.* Plioc., N. Amer.

Galictis. Tayra, Grison. C. Amer., S. Amer.

Putorius. Weasel, Ferret. N. Amer. (since U. Mioc.) to Peru, Eur. (since Plioc.), N. Afr., As., E. Indies.

Gulo. Wolverine. N. As., N. Eur., Greenland, N. U.S.A. (Pleist., Eur.).

SUBFAM. Melinæ. Badgers and Skunks.

† *Trochictis.* Primitive Badger. M. Mioc. to M. Plioc., Eur.

† *Promeles.* Primitive Badger. L. Plioc., Eur.

† *Promephitis.* Primitive Skunk. L. Plioc., Eur.

† *Brachyprotoma.* Primitive Skunk. Pleist., N. Amer.

Mephitis. Skunk. N. Amer. (since Pleist.), C. Amer.

Spilogale. Spotted Skunk. U.S.A., Mexi., C. Amer. (Pleist., N. Amer.)

Conepatus. South American Skunk. S. Amer. to California, (Pleist., S. Amer.).

Meles. European Badger. Eur., As. (U. Mioc., Eur. and As.).

Mellivora. Ratel or Honey Badger. Afr., S. As. (L. Plioc., As.).

Mydaus. Malayan Badger. E. Indies.

Taxidea. American Badger. N. Amer. (since Pleist.).

Arctonyx. Sand Badger. China, Indo-China.

Zorilla. African Polecat. Afr., As. Min. (? Mioc., Eur.).

Helictis. Ferret Badger. China, Indo-China, E. Indies.

SUBFAM. Lutrinæ. Otters.

† *Potamotherium* († *Lutrictis*). Primitive Otter. U. Olig. to L. Mioc., Eur.

† *Enhydriodon.* Primitive Otter. U. Mioc., Eur.; L. Plioc., As.

Lutra. Otter. N. Amer., S. Amer., Eur., As., Afr. (Since U. Mioc., N. Amer. & Eur.; L. Plioc., As.)

Latax. Sea Otter. Pacific Coast of N. Amer. & N. As.

(2) SECTION *ÆLUROIDEA.* Civets, Hyænas, Cats, etc.

FAM. **Viverridæ.** Viverrines.

SUBFAM. Euplerinæ. Insectivorous Viverrids.

Eupleres. Falanouc. Madag.

SUBFAM. Viverrinæ. Civets, etc.

† *Progenetta.* M. to U. Mioc., Eur.

Nandinia. African Palm Civet. W. & C. Afr.

Viverra. True Civet. Afr., S. As., E. Indies (M. Mioc., Eur.[1]).

Genetta. Genet. Afr., Spain, France, Turkey to Arabia.

Linsanga. Linsang. Himalayas to Borneo.

Paradoxurus. Palm Civet. China, India, Indo-China, E. Indies.

Arctictis. Binturong. Himalayas to Borneo.

Arctogale. Small-toothed Palm Civet. E. Indies, Indo-China.

Hemigale. Hemigale. E. Indies.

Cynogale. Cynogale. E. Indies.

SUBFAM. Herpestinæ. Mungooses, etc.

[1] Also recorded from U. Eoc. and L. Olig., Europe, but probably wrongly identified with the modern genus.

Herpestes. Mungoose. Afr., Spain, As. Min., S. As., E. Indies (since U. Olig., Eur.).

Crossarchus. Banded Mungoose, Cusimanse. Afr.

Helogale. Atkinson's Mungoose. E. & S. Afr.

Cynictis. Thick-tailed Mungoose. S.E. Afr.

Suricata. Meerkat. S.E. Afr.

Galidictis. Munguste. Madag.

Galidia. Galidia. Madag.

Hemigalidia. Hemigalidia. Madag.

Subfam. Cryptoproctinæ. Fossa.

Cryptoprocta. Fossa. Madag.

Subfam. Inc. (transitional to Hyænidæ).

† *Ictitherium.* U. Mioc., Eur.

Fam. **Protelidæ.** Aard Wolves.

Proteles. Aard Wolf. S. & E. Afr.

Fam. **Hyænidæ.** Hyænas.

† *Lycyæna.* U. Mioc. to L. Plioc., Eur. & As.

† *Hyænictis.* L. Plioc., Eur. & As.

Hyæna. Striped and Spotted Hyænas. Afr., Syria to India (U. Mioc. to Pleist., Eur.; L. Plioc., As.).

Fam. **Felidæ.** Cats.

Subfam. Machærodontinæ. Saber-tooth Cats.

† '*Ælurogale*' (= *Æluractis*). L. Olig., Eur.

† *Dinictis.* L. to U. Olig., N. Amer.

† *Nimravus.* U. Olig., N. Amer.

† *Hoplophoneus.* M. to U. Olig., N. Amer.

† *Eusmilus.* L. Olig., Eur.; U. Olig., N. Amer.

† *Machairodus.* L. Mioc. to L. Pleist., Eur.; Plioc., As.

† *Smilodon.* Pleist., N. Amer. & S. Amer.

Subfam. Felinæ. True Cats.

† *Pseudælurus.* M. Mioc., Eur. & N. Amer.

† *Hyænælurus.* M. Mioc., Eur.

Felis. Tiger, Lion, Leopard, Puma, Cat, etc. Eur. (since M. Mioc.); As. (since L. Plioc.); N. Amer. (since L. Plioc.); S. Amer. (since Pleist.); Afr.

Lynx. Lynx, Caracal. Eur., As., N. Amer., N. Afr.

Cynælurus. Cheetah or Hunting Leopard. Afr., Syria to India (since L. Plioc.).

3. Suborder **Pinnipedia.** Seals, Walruses, etc.[1]

Fam. **Otariidæ.** Eared Seals.

† *Arctophoca.* (?) L. Mioc., S. Amer.

Otaria. Southern Sea Lion. Coast of Peru, Chili, Argentine (since Pleist.).

Eumetopias. Steller's Sea Lion. Behring Str. to California & to Japan.

Zalophus. California Sea Lion. Coast of California, Austral., N. Zealand, S. Japan (Plioc., Austral.).

Callotaria. Fur Seal or Sea Bear. Behring Str. to S. California & to Japan.

Arctocephalus. Southern Sea Bear. Coast of S. Amer. (E. & W.), E. Afr., Austral., N. Zealand.

Fam. **Odobænidæ.** Walruses.

† *Alactherium.* U. Mioc., Eur.

† *Prorosmarus.* U. Mioc., N. Amer.

Odobœnus. Walrus. Arct., N. Atlant., N. Pacif. Oceans (Plioc., Eur.; Pleist., N. Amer.).

Fam. **Phocidæ.** Earless Seals.

† *Monatherium.* Mioc., Eur.

† *Prophoca.* Mioc., Eur.

† *Pristiphoca.* Plioc., Eur.

Phoca. Harbor Seal, Greenland Seal. Coast of Eur. (since U. Mioc.); N. As., N. Amer., E. & W. (since Mioc.).

Hystriophoca. Ribbon Seal. N. Pacif. Ocean (E. & W.).

Halichœrus. Gray Seal. Coast of Greenland & E. Canada.

Monachus. Monk Seal, West Indian Seal. Mediter., Gulf of Mexi., W. Indies.

Cystophora. Hooded Seal. Arct. & N. Atlant. Oceans (E. & W.).

'*Macrorhinus*' (= *Rhinophoca*). Elephant Seal. E. Pacif. (N. & S.), Indian Oc., S. Austral.

Ogmorhinus. Leopard Seal. Antarct. Oc., S. Austral., N. Zealand, Patagonia.

Lobodon. Crab-eating Seal. Antarct. Oc., S.E. coast of S. Amer.

Leptonychotes. Weddell's Seal. Antarct. Oc., S.E. coast of S. Amer.

Ommatophoca. Ross's Seal. Antarct. Oc.

[1] *Vide* Flower and Lydekker, Introduction to the Study of Mammals, 1891.

VII. Order **RODENTIA**. Rodents.[1]

1. Suborder **Duplicidentata**. Hares and Picas.

Fam. **Lagomyidæ** (= Ochotonidæ). Picas, Mountain Hares.

† *Titanomys*. M. Olig. to L. Mioc., Eur.

† *Prolagus*. L. Mioc. to Pleist., Eur.

Lagomys (= *Ochotona*). Pica. Mountains of Russia, Asia, W. N. Amer. (U. Mioc. to Pleist., Eur.; Pleist., N. Amer.).

Fam. **Leporidæ**. Hares, Rabbits.

† *Palæolagus*. L. Olig., N. Amer.

Lepus. Hare, Rabbit. N. Amer. (since U. Olig.); Eur. & As. (since L. Plioc.); S. Amer., Afr.

Macrotolagus. Jack Rabbit. S.W. U.S.A., Mexi.

Romerolagus. Mexican Cottontail. Mexi.

2. Suborder **Simplicidentata**. Rodents Proper.

(1) Section *SCIUROMORPHA*. Squirrel-like Rodents.

Superfam. *APLODONTOIDEA*. Primitive Sciuromorphs.

Fam. **Ischyromyidæ**. Ischyromyids, Primitive Sciuroids.

† *Paramys*. L. to U. Eoc., N. Amer.

† *Plesiarctomys*. U. Eoc., Eur.

† *Sciuravus*. L. to U. Eoc., N. Amer.

† *Pseudotomus*. M. Eoc., N. Amer.

† *Cylindrodon*. L. Olig., N. Amer.

† *Ischyromys*. L. to M. Olig., N. Amer.

† *Prosciurus*. L. to M. Olig., N. Amer.

Fam. **Pseudosciuridæ**. Pseudosciurids.

† *Sciuroides*. L. Olig., Eur.

† *Pseudosciurus*. Olig., Eur.

† *Sciurodon*. L. Olig., Eur.

† *Eomys*. U. Eoc., Eur.

† *Phiomys*. L. Olig., N. Afr. (Fayûm).

† *Metaphiomys*. L. Olig., N. Afr. (Fayûm).

† *Rhodanomys*. U. Olig., Eur.

Fam. **Aplodontiidæ**. Sewellels.

† *Meniscomys*. U. Olig., N. Amer.

† *Mylagaulodon*. U. Olig., N. Amer.

Aplodontia. Sewellel. N.W. N. Amer. (since Pleist.).

[1] *Vide* Tullberg, T., Ueber das System der Nagethiere, Upsala, 1899; Weber, M., Die Säugetiere, 1904; Beddard, Mammalia, 1902; Hornaday, The American Natural History, 1904. The present arrangement is by Matthew.

FAM. **Mylagaulidæ**. Horned Gophers.

† *Mesogaulus*. M. Mioc., N. Amer.

† *Mylagaulus*. M. Mioc. to L. Plioc., N. Amer.

† *Ceratogaulus*. M. Mioc., N. Amer.

† *Epigaulus*. L. Plioc., N. Amer.

SUPERFAM. *SCIUROIDEA*. Sciuroids.

FAM. **Sciuridæ**. Squirrels.

SUBFAM. Nannosciurinæ. Pigmy Squirrels.

Nannosciurus. Afr., Philipp., Indo-Austral.

SUBFAM. Arctomyinæ. Marmots, Woodchuck, etc.

† *Palæarctomys*. U. Mioc., N. Amer.

Spermophilus. Spermophile, Suslik. E. Eur., Siberia, W. N. Amer.

'*Arctomys*' (= *Marmota*). Marmot, Woodchuck, etc. N. Amer. (since U. Mioc.); Eur. (since Pleist.), N. & C. As.

Cynomys. Prairie Dog. C. U.S.A. (since U. Mioc.).

SUBFAM. Sciurinæ. True Squirrels, Chipmunks, etc.

Sciurus. Squirrel. Temperate and Trop. Regions of the World, exc. Austral. and Madag. (since U. Olig., Eur. & N. Amer.).

Tamias. Chipmunk. E. & C. U.S.A. (since Pleist.), S. Canada.

SUBFAM. Xerinæ. Spiny Squirrels, Giant Squirrels.

Xerus. Spiny Squirrel. Afr.

Ratufa. Giant Squirrel. India, Indo-China, E. Indies.

SUBFAM. Pteromyinæ. Flying Squirrels.

Pteromys. Larger Flying Squirrel. C. & S.E. As., E. Indies.

Sciuropterus. Lesser Flying Squirrel. N. Amer., As., Eur.

Eupetaurus. Woolly Flying Squirrel. Thibet.

SUPERFAM. *CASTOROIDEA*. Beavers and Beaver-like Rodents.

FAM. **Castoridæ**. Beavers.

† *Eutypomys*.[1] M. Olig., N. Amer.

† *Steneofiber*. M. Olig. to M. Mioc., Eur.; U. Olig., N. Amer.

† *Euhapsis*. U. Olig., N. Amer.

† *Chalicomys*. U. Mioc. to Plioc., Eur.

† '*Dipoides*' (= *Eucastor*). U. Mioc. to Plioc., Eur., As., & N. Amer.

† *Hystricops*. U. Mioc. to L. Plioc., N. Amer.

Castor. Beaver. N. Amer. (since Pleist.); Eur. (since Plioc.); W. As.

† *Trogontherium*. Pleist., Eur.

[1] Possibly related to Pteromyinæ.

FAM. **Castoroïdidæ**. Beaver-like Rodents.

† *Castoroïdes*. Pleist., N. Amer.

† *Amblyrhiza*. Pleist., W. Indies.

SUPERFAM. *GEOMYOIDEA*. Pocket Gophers, Pocket Mice, Kangaroo Rats, etc.

FAM. **Heteromyidæ**. Kangaroo Rats & Pocket Mice.

† '*Gymnoptychus*' (= *Adjidaumo*). L. to U. Olig., N. Amer.

† *Heliscomys*. M. Olig., N. Amer.

Perognathus. Pocket Mouse. U.S.A., Mexi. (? L. Mioc., N. Amer.).

Heteromys. Pouched Spiny Rat & Mouse. Mexi. to Ecuador & Venezuela.

Dipodomys. Kangaroo Rat. U.S.A., Mexi.

FAM. **Geomyidæ**. Pocket Gophers.

† *Inc. sed. Protoptychus*. U. Eoc., N. Amer.

† *Entoptychus*. U. Olig. to L. Mioc., N. Amer.

† *Pleurolicus*. U. Olig., N. Amer.

Thomomys. Lesser Pocket Gopher. U.S.A., Mexi. (since M. Mioc., N. Amer.).

Geomys. Pocket Gopher. U.S.A., Mexi. (since U. Mioc., N. Amer.).

(2) SECTION *MYOMORPHA*. Rat-like Rodents.

SUPERFAM. *MYOIDEA*. Rats, Jerboas, etc.

FAM. '**Gliridæ**' (= Myoxidæ). Dormice.

Myoxus. Squirrel-tailed & Garden Dormouse. Eur. (since U. Olig.); S.W. As., Japan.

Graphiurus. African Dormouse. Afr.

Platacanthomys. Malabar Spiny Mouse. S. India, Cochinchina.

Muscardinus. Common Dormouse. Eur. (since Pleist.), As. Min.

Eliomys. Lerot. Eur., N. Afr.

FAM. **Muridæ**. Rats, Mice, etc.

SUBFAM. 'Cricetinæ' (= Sigmodontinæ). Hamsters, Field Mice, and Field Rats.

† *Cricetodon*. L. Olig. to U. Mioc., Eur.

† *Eumys*. M. to U. Olig., N. Amer.

SUBFAM. Murinæ. Rats and Mice.

Mus. Rat, Mouse. Cosmop. (Plioc. & Pleist., Eur.).

Nesocia. Bandicoot Rat. Palestine to Java (Plioc. & Pleist., India).

Acomys. Spiny Mouse. E. Afr., As. (U. Mioc & Plioc., Eur.).

Chiruromys. Prehensile-tailed Mouse. N. Guin.

Uromys, Hapalotis, Mastacomys. Jerboa Rats. Australia.

Cricetomys. Giant Rat. E., W. & S. Afr.

Saccostomus. Pouched Rat. S. Afr.

Subfam. Gerbillinæ. Gerbilles.

Gerbillus. Gerbille, Afr., Russia, W. As. to China (Pleist., India).

Psammomys. Sand Rat. N. Afr., Palestine.

Meriones. Shaw's Mouse. S.E. Russ., N. Afr. to C. Asia.

Subfam. Hydromyinæ. Australian Water Rats.

Hydromys. Australian Water Rat. Austral., N. Guin.

Xeromys. Queensland Rat. Queensland.

Subfam. Phlæomyinæ. Philippine Rats, etc.

Phlœomys. Philippine Rat. Philippines.

Carpomys. Philippine Fruit Mouse. Philippines.

Subfam. Rhynchomyinæ. Shrew Rats.

Celœnomys, Chrotomys, etc. Philippine Mice. Mountains of Luzon.

Rhynchomys. Shrew Rat. Philippines.

Subfam. Otomyinæ. Otomyins.

Otomys. Otomys. S. & E. Afr.

Subfam. Dendromyinæ. African Tree Mice.

Dendromys. African Tree Mouse. Afr.

Subfam. Lophiomyinæ. Crested Hamsters.

Lophiomys. African Crested Hamster. N.E. Afr.

Subfam. Microtinæ. Voles, or Meadow Mice.

Microtus. Meadow Mouse, or Vole. Eur. (since Plioc.); W. & C. As., N. Amer. (since Pleist.).

Arvicola. Water Vole. Palæarctic (since Pleist.).

Myodes. Lemming. N. Amer., N. Eur. (Pleist., Eur., N. Amer.).

Cuniculus. Banded Lemming. Arctic Eur., As., N. Amer. (Pleist., Eur.).

Evotomys. Red-backed Vole. N. Eur., Siberia, N. Amer.

Fiber. Musk Rat. Canada, U.S.A. (since L. Pleist.).

Phenacomys. Mountain Vole. N. Amer.

Peromyscus (*Hesperomys*). Field Mouse. N. Amer. (since Mioc.).

Cricetus. Hamster. Eur. to C. As. (since Plioc., Eur.).

Sigmodon. Cotton Rat. S. U.S.A. to Peru (Pleist., S. Amer.).

Oryzomys. Rice Rat. S. Amer., S. & E. U.S.A.

Reithrodontomys. Harvest Mouse. U.S.A.

Ichthyomys. Fish-eating Rat. N. S. Amer. to Panama.

Eliurus. Madagascan Rat. Madag.

Reithrodon. Reithrodon. S. Amer. (since Pleist.).

Neotoma. Wood Rat, Pack Rat. N. Amer. (since Pleist.); C. Amer.

Hodomys. Allen's Wood Rat. Mexi.

FAM. **Spalacidæ.** Mole Rats.

Spalax. Egyptian Mole Rat. S. Russia, Balkan Penin., Egypt to Turkestan. (Eur. since Mioc.)

Rhizomys. Bamboo Rat. Thibet, China to Sumatra.

FAM. **Dipodidæ.** Jerboas and Jumping Mice.

† *Protoptychus.* U. Eoc., N. Amer.

† *Paciculus.* U. Olig., N. Amer.

Zapus. Jumping Mouse. U.S.A., Canada, China (Pleist., N. Amer.).

Alactaga. Five-toed Jerboa. Russ., As. Min. to China, N. Afr. (Pleist. Eur.)

Dipus. True Jerboa. N. Afr., C. & S.W. As.

Sminthus. Sminthus. E. Eur., W. & C. As. (Pleist., Eur.).

SUPERFAM. '*ANOMALUROIDEA.*' Anomaluroids.

FAM. **Pedetidæ.** Spring Haas Family.

Pedetes. Cape Spring Haas. S. Afr.

FAM. **Anomaluridæ.** African Flying Squirrels.

Anomalurus. African Flying Squirrel. Afr.

Idiurus. Long-tailed African Flying Squirrel. S.W. Afr.

SUPERFAM. *BATHYERGOIDEA.* Bathyergoids.

FAM. **Bathyergidæ.** Cape Mole Rats.

Bathyergus. Large Cape Mole Rat. S. Afr.

Heterocephalus. Naked Sand Rat. Abyssinia, Somali.

Georhychus. Blesmol. S. & W. Afr.

(3) SECTION *HYSTRICOMORPHA.* Porcupine-like Rodents.

FAM. **Theridomyidæ.** Ancestral Hystricomorphs.

† *Trechomys.* M. Eoc. to L. Olig., Eur.

† *Protechimys.* L. Olig., Eur.

† *Theridomys.* U. Eoc. to L. Mioc., Eur.

† *Issiodoromys*. M. Olig., Eur.

† *Nesokerodon*. U. Eoc., Eur.

† *Archæomys*. U. Olig., Eur.

Fam. **Ctenodactylidæ**. African Jumping Mice.

Ctenodactylus. African Gundi. N. Afr.

Pectinator. Speke's Jumping Mouse. Abyssinia.

Fam. **Octodontidæ**. Coypu and Spiny Rats.

Subfam. Octodontinæ. Tuco-tucos, etc.

Octodon. Degu. W. S. Amer.

Ctenomys. Tuco-tuco. S. Amer., S. of Amazon (since Plioc.).

Petromys. African Rock Rat. S. Afr.

Subfam. Loncherinæ. Spiny Rats.

† *Spaniomys*. U. Mioc., S. Amer.

† *Stichomys*. U. Mioc., S. Amer.

Echinomys. Spiny Rat. Paraguay to Panama.

Loncheres. Porcupine Rat. Paraguay to Venezuela (since Pleist.).

Subfam. Capromyinæ. Water Rats, Tree Rats, Cane Rats.

† *Neoreomys*. U. Mioc., S. Amer.

† *Scleromys*. U. Mioc., S. Amer.

'*Myocastor*' (= *Myopotamus*). Coypu or Water Rat. S. & C. S. Amer. (since Plioc.).

Capromys. Cuban Tree Rat or Hutia. W. Indies, Bahamas.

Aulacodus. African Cane Rat. W., E. & S. Afr.

Fam. **Hystricidæ**. Porcupines.

Subfam. Erethizontinæ. New World Porcupines.

† *Acaremys*. U. Mioc., S. Amer.

† *Steiromys*. U. Mioc., S. Amer.

Erethizon. Canada Porcupine. Alaska & Labrador to Arizona (Pleist., N. Amer.).

'*Synetheres*' (= *Cercolabes*). Tree Porcupine. Bolivia to Mexi., W. Indies.

Chætomys. Thin-spined Porcupine. Brazil.

Subfam. Hystricinæ. Old World Porcupines.

Hystrix. True Porcupine. Afr., S. Eur., S. As., E. Indies (M. Mioc., Eur.).

Atherura. Brush-tailed Porcupine. Indo-China, W. Afr. (Pleist., India).

Fam. **Chinchillidæ**. Viscachas, Chinchillas.

† *Prolagostomus*. U. Mioc., S. Amer.

† *Perimys.* Mioc., S. Amer.

† *Megamys.* Giant Chinchilla. Plioc., Argentina.

† *Amblyrhiza.* Giant Chinchilla. Pleist., W. Indies.

Chinchilla. Chinchilla. Andes Mts.

Lagostomus. Viscacha. Argentine (since Plioc.).

Lagidium. Four-toed Chinchilla. Andes Mts.

Fam. **Dinomyidæ.** Long-tailed Pacas.

Dinomys. Branick's Paca. Peru.

Fam. **Dasyproctidæ.** Agoutis.

Cœlogenys. Paca. Paraguay to C. Amer. (Pleist., S. Amer.).

Dasyprocta. Agouti. Paraguay to Mexi. (Pleist., S. Amer.).

Fam. **Caviidæ.** Cavies.

† *Eocardia.* U. Mioc., S. Amer.

† *Schistomys.* U. Mioc., S. Amer.

Cavia. Guinea Pig. S. Amer. (since Plioc.).

Hydrochœrus. Capybara. Guiana to Uruguay (since Plioc.).

Dolichotis. Patagonian Cavy. Argentine (since Plioc.).

Inc. Sed.

† *Cephalomys.* Eoc., S. Amer.

Inc. Sed. Edentata.

VIII. Order **TÆNIODONTA.** Tæniodonts (Ganodonts), primitive Edentates with enameled teeth.[1]

Fam. **Conoryctidæ.** Conoryctids.

† *Onychodectes.* Bas. Eoc., N. Amer.

† *Conoryctes.* Bas. Eoc., N. Amer.

Fam. **Stylinodontidæ.** Stylinodonts.

† '*Hemiganus*' (= *Wortmania*). Bas. Eoc., N. Amer.

† *Psittacotherium.* Bas. Eoc., N. Amer.

† *Calamodon.* L. Eoc., N. Amer.

† *Stylinodon.* L. to M. Eoc., N. Amer.

IX. Order '**EDENTATA**' (Xenarthra). American Edentates.[2]

1. Suborder '**Pilosa**' (= Anicanodonta). Hairy Edentates.

[1] *Vide* Wortman, J. L. The Ganodonta and their Relationship to the Edentata. *Bull. Amer. Mus. Nat. Hist.*, Vol. IX, 1897, pp. 59–110. The supposed ancestral relationship of the Ganodonta (Tæniodonta) to the Edentates is denied by Scott (Mammalia of the Santa Cruz Beds, Edentata. *Princeton University, Exped. to Patagonia*, Vol. V, 1903–1905).

[2] *Vide* Flower and Lydekker, Introduction to the Study of Mammals, 1892; Weber, Die Säugetiere, 1900; Scott, Mammalia of the Santa Cruz Beds, Edentata. *Princeton Patagonian Exped.*, Vol. V. The present arrangement is by Osborn and Matthew.

(1) Section *GRAVIGRADA*. Ground Sloths.

Fam. **Megalonychidæ**. Tusked Ground Sloths.

Subfam. Megalonychinæ. Megalonyx, etc.

† *Hapalops*. U. Mioc., S. Amer.

† *Pelecydon*. U. Mioc., S. Amer.

† *Schismotherium*. U. Mioc., S. Amer.

† *Planops*. U. Mioc., S. Amer.

† *Prepotherium*. U. Mioc., S. Amer.

† *Eucholœops*. U. Mioc., S. Amer.

† *Megalonychotherium*. U. Mioc., S. Amer.

† *Megalonyx*. Plioc., N. Amer.

Subfam. Mylodontinæ. Mylodon, etc.

† *Nematherium*. Mioc., S. Amer.

† *Analcitherium*. U. Mioc., S. Amer.

† *Scelidotherium*. Plioc. to Pleist., S. Amer.

† '*Lestodon*' (= *Pseudolestodon*). Plioc. & Pleist., S. Amer.

† *Catonyx*. Pleist., S. Amer.

† *Mylodon*. Pleist., N. & S. Amer.

† '*Glossotherium*' (= *Neomylodon*, *Grypotherium*). Pleist., S. Amer.

† *Paramylodon*. Pleist., N. Amer.

Fam. **Megatheriidæ**. Megatheres or Giant Ground Sloths.

† *Megatherium*. Plioc. & Pleist., S. & C. Amer.; Pleist., N. Amer.

† *Nothrotherium*. Pleist., S. Amer.

(2) Section *VERMILINGUA*. Anteaters.

Fam. **Myrmecophagidæ**. American Anteaters.

Tamandua. Tamandua. Argentine to Mexi.

Myrmecophaga. Great Anteater. Argentine to C. Amer.

'*Cycloturus*' (= *Cyclopes*). Little Anteater. N. S. Amer. to C. Amer.

(3) Section *TARDIGRADA*.

Fam. **Bradypodidæ**. Sloths.

Bradypus. Ai, Three-toed Sloth. Bolivia to C. Amer.

Cholœpus. Unau, Two-toed Sloth. Ecuador to Costa Rica.

2. Suborder '**Loricata**' (= Hicanodonta). Armored Edentates.

(1) Section *DASYPODA*. Armadillos.

Fam. **Metacheiromyidæ**. Middle Eocene Armadillos.

† *Metacheiromys*. M. Eoc., N. Amer.

FAM. **Dasypodidæ**. Fossil and Recent Armadillos.

SUBFAM. Dasypodinæ. Six-, Seven-, Eight-, Eleven-banded, Giant Armadillo, etc.

† *Proeutatus*. U. Mioc., S. Amer.

† *Prozaëdius*. U. Mioc., S. Amer.

† *Stenotatus*. U. Mioc., S. Amer.

† *Eutatus*. Pleist., S. Amer.

† *Chlamydotherium*. Pleist., S. Amer.

Dasypus. Six-, Seven-, and Eight-banded Armadillos. S. Amer.

Xenurus. Cabassou, Eleven-banded Armadillo. Paraguay to C. Amer.

Priodon (= *Priodontes*). Giant Armadillo. Argentine to Guiana.

Tolypeutes. Apar. Argentine to Guiana.

Zaëdius. Pichi, Peludo. S. S. Amer.

SUBFAM. Chlamydophorinæ. Pichiciagos.

Chlamydophorus. Pichiciago. W. Argentine.

SUBFAM. Tatusiinæ. Peba Armadillo, etc.

† *Stegotherium*. U. Mioc., S. Amer.

'*Tatusia*' (= *Tatu*). Peba, Nine-banded Armadillo. Argentine to Texas (Pleist., S. Amer.).

SUBFAM. Peltephilinæ. Peltephilins.

† *Peltephilus*. U. Mioc., S. Amer.

SUBFAM. Scleropleurinæ. Scleropleurins.

Scleropleura. Scleropleura. Brazil.

(2) SECTION *GLYPTODONTIA*. Tortoise Armadillos.

FAM. **Glyptodontidæ**. Glyptodons.

SUBFAM. Glyptodontinæ. Glyptodons Proper.

† *Propalæohoplophorus*. U. Mioc., S. Amer.

† *Cochlops*. U. Mioc., S. Amer.

† *Eucinepeltus*. U. Mioc., S. Amer.

† *Glyptodon*. Plioc., S. Amer., N. Amer.

† *Glyptotherium*. Plioc., N. Amer.

SUBFAM. Dœdicurinæ. Dœdicurins.

† *Dœdicurus*. Pleist., S. Amer.

SUBFAM. Sclerocalyptinæ. Sclerocalyptins.

† '*Sclerocalyptus*' (= *Hoplophorus*). Plioc. to Pleist., S. Amer.

† *Panochthus*. Pleist., S. Amer.

X. Order **PHOLIDOTA**. Scaly Anteaters.[1]

Fam. **Manidæ**. Pangolins.

† *Leptomanis*. M. Olig., Eur., Afr.

Manis. Pangolin. W. Afr.

Pholidotus. Long-tailed Pangolin. W., S., & E. Afr., S.E. As. to Celebes (Plioc., As.).

XI. Order **TUBULIDENTATA**. Aard Varks.[2]

Fam. **Orycteropodidæ**. Aard Varks.

† *Palæorycteropus*. U. Mioc., Eur., Afr.

Orycteropus. Aard Vark, Afr.

b. Cohort PRIMATES. Mostly Arboreal Mammals with 'nails' as distinguished from mammals with claws (Unguiculates) or hoofs (Ungulates).[3]

XII. Order **PRIMATES**. Primates.

1. Suborder **Lemuroidea**. Lemuroids.

Fam. **Notharctidæ**. Notharctids or Extinct Lemur-like Primates.

† *Pelycodus*. L. to M. Eoc., N. Amer.

† *Notharctus*. L. to U. Eoc., N. Amer.

† (?) *Cænopithecus*. U. Eoc., Eur.

Fam. **Anaptomorphidæ**. Anaptomorphids or Extinct Tarsius-like Primates.

† *Anaptomorphus*. L. to M. Eoc., N. Amer.

† *Omomys*. M. Eoc., N. Amer.

† *Hemiacodon*. M. Eoc., N. Amer.

† *Washakius*. M. Eoc., N. Amer.

† *Necrolemur*. U. Eoc., Eur.

† (?) *Microchœrus*. U. Eoc., Eur.

Fam. **Adapidæ**. Adapids.

† *Plesiadapis*. L. Eoc., Eur.

† *Adapis*. M. Eoc. to L. Olig., Eur.

Inc. Sed.

† *Protoadapis*. L. Eoc., Eur.

† *Notopithecus*. U. Mioc., S. Amer.

† *Homunculus*. U. Mioc., S. Amer.

[1] *Vide* Weber, Die Säugetiere, 1904.

[2] *Vide* Weber, Die Säugetiere, 1904.

[3] For the recent primates, see especially: Flower and Lydekker, *op. cit.* 1892; Beddard, *op. cit.* 1902; Weber, *op. cit.* 1904. The Eocene primates of North America are described especially by Osborn (*Bull. Amer. Mus. Nat. Hist.*, Vol. XVI, 1902, pp. 169–214) and Wortman (*Amer. Jour. Sci.*, Vol. XV, 1903, pp. 419, *et seq.*). For extinct lemurs of Madagascar, see Grandidier, Recherches sur les Lémuriens disparus, etc. *Nouv. Arch. du Mus.*, Ser. 4, Vol. VII, Paris, 1905.

FAM. **Lemuridæ**. Lemurs.

SUBFAM. Indrisinæ. Indris.

Indris. Indris or Babakato. Madag.

Propithecus. Propitheque. Madag.

Avahis. Avahi or Woolly Lemur. Madag.

SUBFAM. Megaladapinæ. Megaladapids.

† *Megaladapis*. Pleist. Madag.

SUBFAM. Archæolemurinæ. Ape-like Lemurs.

† *Archæolemur*. Pleist. Madag.

SUBFAM. Lemurinæ. True Lemurs.

Lemur. Lemur. Madag. (since Pleist.).

Hapalemur. Gray Lemur. Madag.

Lepidolemur. Weasel Lemur. Madag.

SUBFAM. Galaginæ. Galagos, Mouse Lemurs, etc.

Galago. Galago. Afr. (except N.W.).

Chirogale. Mouse Lemur. Madag.

Microcebus. Dwarf Lemur. Madag.

SUBFAM. Lorisinæ. Slow Lemurs.

Loris. Slender Loris. S. India, E. Burma.

Nycticebus. Gray Loris. N. India to Philippines.

Perodicticus. Potto. W. Afr.

Arctocebus. Angwantibo. W. Afr.

FAM. '**Chiromyidæ**' (= Daubentoniidæ). Aye-ayes.

'*Chiromys*' (= *Daubentonia*). Aye-aye. Madag.

FAM. **Tarsiidæ**. Tarsiers.

Tarsius. Spectral Tarsier. E. Indies.

2. SUBORDER **ANTHROPOIDEA**. Monkeys, Apes, Man.

Platyrrhine or 'Broad Nostril' Group (New World).

FAM. **Hapalidæ**. Marmosets.

Midas. Tamarin. Brazil to C. Amer.

Hapale. Short-tusked Marmosets. S. Brazil to Colombia.

FAM. **Cebidæ**. South American Monkeys.

Cebus. Capuchin. S. Brazil to C. Amer. (Pleist., S. Amer.).

Lagothrix. Woolly Monkey. N. S. Amer.

Mycetes. Howler. S. Amer. to Mexi. (Pleist., S. Amer.).

Ateles. Spider Monkey. Brazil to S. Mexi.

Nyctipithecus. Douroucoli. N. Argentine to C. Amer.

Chrysothrix. Squirrel Monkey. Bolivia to C. Amer.

Callithrix. Titi Monkey. E. Brazil to Colombia (Pleist., S. Amer.).

Pithecia. Saki. N. S. Amer.

Uacaria. Uakari. Brazil.

Catarrhine or 'Narrow Nostril' Group (Old World).

Fam. **Cercopithecidæ.** Old World Monkeys.

Subfam. Cercopithecinæ. Baboons, Guenons, Mangabeys, etc.

† *Oreopithecus.* M. Mioc., Eur.

Macacus. Macaque. E. & S. As., E. Indies, N. Afr., Gibraltar (Plioc. to Pleist., Eur., As.; Pleist., N. Afr.).

Cynopithecus. Celebes 'Black Ape.' Celebes.

'*Cynocephalus*' (= *Papio*). Baboon. W. & S. Afr. to Arabia (Plioc. to Pleist., India; Pleist., N. Afr.).

Cercocebus. Mangabey. W. & E. Afr.

Cercopithecus. Guenon. Afr. (exc. N.W.).

Subfam. Semnopithecinæ. Langurs, Thumbless Monkeys, etc.

† *Mesopithecus.* L. Plioc., Eur.

† *Dolichopithecus.* Plioc., Eur.

Semnopithecus. Langur. India to E. Indies (Plioc., Eur. & As.).

Nasalis. Proboscis Monkey. Borneo.

Colobus. Colob, Guereza, etc. E. & W. Afr.

Fam. **Simiidæ.** Anthropoid Apes.

† *Dryopithecus.* M. to U. Mioc., Eur.

† *Pliopithecus.* Ancestral Gibbon. L. Mioc. to L. Plioc., Eur.

† *Anthropodus.* U. Mioc., Eur.

Hylobates. Gibbon. S.E. As. to E. Indies.

Simia. Orang-Utan. Borneo, Sumatra (Plioc., As.).

Gorilla. Gorilla. W. & E. Afr.

Anthropopithecus. Chimpanzee. C. Afr. (Plioc., As.).

Fam. **Hominidæ.** Mankind.

† *Pithecanthropus.* Pleist., As. (Java).

Homo. Man. Whole World.

c. Cohort UNGULATA. Hoofed Mammals.

XIII. Order **CONDYLARTHRA.** Condylarths or Slender Archaic Ungulates.[1]

[1] *Vide* Cope [Description of *Phenacodus*]. The Vertebrata of the Tertiary Formations of the West. *Rept. U.S. Geol. Surv.*, Washington, 1884; Osborn, Remounted Skeleton of *Phenacodus primævus*, etc. *Bull. Amer. Mus. Nat. Hist.*, Vol. X, 1898, pp. 159–164; Matthew [On Euprotogonia and the relationships and classification of the Condylarthra], *Bull. Amer. Mus. Nat. Hist.*, Vol. IX, 1897, pp. 259–323.

Inc. Sed. Fam. **Mioclænidæ**. Mioclænids.

† *Mioclænus*. Bas. Eoc., N. Amer.

Inc. Sed. Fam. **Pleuraspidotheriidæ**. Pleuraspidotheres.

† *Pleuraspidotherium*. L. Eoc., Eur.

Fam. **Meniscotheriidæ**. Meniscotheres.

† *Meniscotherium*. L. Eoc., N. Amer.

Fam. **Phenacodontidæ**. Phenacodonts or Slender-footed, Archaic Ungulates.

† *Protogonodon*. Bas. Eoc., N. Amer.

† *Euprotogonia*. Bas. Eoc., N. Amer.

† *Phenacodus*. L. Eoc., N. Amer.

† *Ectocion*. L. Eoc., N. Amer.

Fam. *Inc.*

† *Didolodus*. Bas. Eoc., S. Amer.

† *Notoprotogonia*. Bas. Eoc., S. Amer.

† *Lambdaconus*. Bas. Eoc., S. Amer.

† *Proëctocion*. Bas. Eoc., S. Amer.

XIV. Order **AMBLYPODA**. Amblypods or Short-footed, Archaic Ungulates.[1]

1. Suborder **Taligrada**. Taligrade Amblypods.

Fam. **Periptychidæ**. Periptychids.

† *Anisonchus*. Bas. Eoc., N. Amer.

† *Haploconus*. Bas. Eoc., N. Amer.

† *Ectoconus*. Bas. Eoc., N. Amer.

† *Conacodon*. Bas. Eoc., N. Amer.

† *Periptychus*. Bas. Eoc., N. Amer.

† *Hemithlæus*. Bas. Eoc., N. Amer.

Inc. Sed. (? Periptychidæ).

† *Guilielmofloweria*. Bas. Eoc., S. Amer.

† *Ricardolydekkeria*. Bas. Eoc., S. Amer.

Fam. **Pantolambdidæ**. Pantolambdids.

† *Pantolambda*. Bas. Eoc., N. Amer.

2. Suborder **Pantodonta**. Pantodont Amblypods (or with a full set of teeth).

[1] *Vide* Cope, The Vertebrata of the Tertiary Formations of the West, 1884 ; Osborn, Evolution of the Amblypoda, Part I. Taligrada and Pantodonta. *Bull. Amer. Mus. Nat. Hist.*, Vol. X, 1898, pp. 169–218 ; Matthew [Osteology of *Euprotogonia* and relationships of the Condylarthra], A Revision of the Puerco Fauna. *Bull. Amer. Mus. Nat. Hist.*, Vol. IX, 1897, pp. 299–308; Marsh, Dinocerata. *Monographs U.S. Geol. Surv.*, Washington, 1884.

FAM. **Coryphodontidæ**. Coryphodonts.

† *Coryphodon*. L. Eoc., N. Amer.

FAM. '**Uintatheriidæ**' (= Eobasileidæ). Eobasileids or Uintatheres.

† *Bathyopsis*. L. Eoc., N. Amer.

† '*Dinoceras*,' '*Tinoceras*' (= *Uintatherium*). M. Eoc., N. Amer.

† '*Loxolophodon*' (= *Eobasileus*). U. Eoc., N. Amer.

XV. ORDER **ARTIODACTYLA**. Even-toed Ungulates.[1]

(1) SECTION *PRIMITIVE ARTIODACTYLS* (families of more or less uncertain affinities).

A. Bunodont families, with conic or incipiently crescentic molar cusps.

FAM. **Trigonolestidæ**. Trigonolestids.

† *Trigonolestes*. L. Eoc., N. Amer.

FAM. **Leptochœridæ**. Leptochœres.

† *Stibarus*. L. to M. Olig., N. Amer.

† *Leptochœrus*. M. to U. Olig., N. Amer.

FAM. **Dichobunidæ**. Dichobunes of Europe, Homacodonts of North America.

† *Dichobune*. M. Eoc., Eur.

† *Mouillacitherium*. M. Eoc., Eur.

† *Homacodon*. M. Eoc., N. Amer.

† *Bunomeryx*. U. Eoc., N. Amer.

Inc. Sed.

† *Microsus*. M. Eoc., N. Amer.

† *Antiacodon*. M. Eoc., N. Amer.

† *Sarcolemur*. M. Eoc., N. Amer.

† *Nanomeryx*. M. Eoc., N. Amer.

† *Helohyus*. M. Eoc., N. Amer.

B. Bunoselenodont families, with combined conic and crescentic molar cusps.

FAM. **Anthracotheriidæ**. Anthracotheres.

† *Lophiobunodon*. M. Eoc., Eur.

† *Catodontherium*. M. Eoc., Eur.

[1] For a general treatment of the Artiodactyla consult the textbooks of Flower and Lydekker, Beddard, Weber, and Cope's article, The Artiodactyla (*Amer. Naturalist*, Vol. XXII, 1888, pp. 1079–1095). The fossil artiodactyls of Europe are treated in Von Zittel's Handbuch der Paläontologie, Mammalia, and in Kowalevsky's Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer natürlichen Classification der fossilen Hufthiere (*Palæontographica*, Bd. XXII, 1873). For a modern view of the interrelationships of the artiodactyl families, consult: Matthew, W. D., A Complete Skeleton of *Merycodus*, *Bull. Amer. Mus. Nat. Hist.*, Vol. XX, 1904, pp. 101–129, and Osteology of *Blastomeryx* and Phylogeny of the American Cervidæ, *idem*, Vol. XXIV, 1908, pp. 535–562. The present arrangement is by Osborn and Matthew.

† *Anthracotherium.* U. Eoc. and Olig., Eur.

† *Arretotherium.* L. Mioc., N. Amer.

† '*Hyopotamus*' (= *Ancodon*). L. Olig. to L. Mioc., N. Afr., Eur., N. Amer.

† *Brachyodus.* L. Mioc., Eur.

† *Merycopotamus.* U. Mioc., As.

C. Selenodont families, with all molar cusps crescentic.

Fam. **Anoplotheriidæ.** Anoplotheres.

Subfam. Anoplotheriinæ. Anoplotheres Proper.

† *Anoplotherium.* U. Eoc. to L. Olig., Eur.

† *Diplobune.* U. Eoc. to L. Olig., Eur.

Subfam. Cænotheriinæ. Cænotheres.

† *Cœnotherium.* L. to U. Olig., Eur.

† *Plesiomeryx.* M. to U. Olig., Eur.

Subfam. Dichodontinæ. Dichodonts.

† '*Dichodon*' (= *Dacrytherium*), U. Eoc. to L. Olig., Eur.

† *Tetraselenodon.* U. Eoc., Eur.

† *Haplomeryx.* U. Eoc., Eur.

Subfam. Xiphodontinæ. Xiphodonts.

† *Xiphodon.* U. Eoc. to L. Olig., Eur.

† '*Xiphodontherium*' (= *Amphimeryx*), U. Eoc. to L. Olig., Eur.

(2) Section *SUINA* or Pig-like Artiodactyls.

Fam. **Suidæ.** Pigs.

† *Cebochœrus.* M. Eoc. to L. Olig., Eur.

† *Chœropotamus.* U. Eoc., Eur.

† *Acotherulum.* U. Eoc., Eur.

† *Propalæochœrus.* M. Olig., Eur.

† *Palæochœrus.* M. Olig. to L. Mioc., Eur.

† *Doliochœrus.* U. Olig., Eur.

† *Hyotherium.* L. to U. Mioc., Eur.

† *Chœrotherium.* M. Mioc., Eur.

† *Listriodon.* L. to U. Mioc., Eur.; L. Plioc., As.

Sus. Pig, Boar. Eur. & As. (since U. Mioc.); E. Indies, N. Guin.; N. & E. Afr. (since Plioc.).

Potamochœrus. Red River Hog, Bosch Vark. Afr. (exc. N.W.); Mioc., Eur. As.

Babirusa. Babirusa. Celebes I.

Hylochœrus. Forest Pig. Afr.

Phacochœrus. Wart Hog. Afr. (exc. N.W.); (Pleist., Algeria and S. Africa).

Fam. '**Dicotylidæ**' (= Tagassuidæ). Peccaries of North America.

† *Thinohyus* (= *Perchœrus*). L. to U. Olig., N. Amer.

† *Chœnohyus.* U. Olig., N. Amer.

† *Desmathyus.* L. Mioc., N. Amer.

† *Prosthennops.* U. Mioc. to L. Plioc., N. Amer.

† *Platygonus.* M. Plioc. to Pleist., N. Amer.

† *Mylohyus.* Pleist., N. Amer.

'*Dicotyles*' (= *Tagassu*). Peccary. Texas to Argentine (since Pleist.).

Fam. **Entelodontidæ**. Entelodonts or Elotheres.

Subfam. Achænodontinæ. Achænodonts.

† *Parahyus.* L. Eoc., N. Amer.

† *Achœnodon.* U. Eoc., N. Amer.

Subfam. 'Elotheriinæ' (= Entelodontinæ). Entelodonts Proper.

† *Entelodon* (incl. *Archœotherium*, *Pelonax*). L. to U. Olig., N. Amer. & Eur.

† *Dœodon.* U. Olig., N. Amer.

† *Boöchœrus.* U. Olig., N. Amer.

† *Dinohyus.* U. Olig., N. Amer.

Fam. **Hippopotamidæ**. Hippopotami.

† *Hexaprotodon.* L. Plioc. to Pleist., As.; U. Plioc., N. Afr.

Chœropsis (= *Hyopotamus*). Pigmy Hippopotamus. Liberia (Pleist., Madagascar, I. Cyprus).

Hippopotamus. Hippopotamus. Afr. (exc. N.W.), (Plioc. & Pleist. Eur., As. and N. Afr.).

(3) Section *OREODONTA*. American Primitive Ruminants.

Fam. '**Oreodontidæ**' (= Agriochœridæ). Oreodonts.

† *Protoreodon.* U. Eoc., N. Amer.

† *Protagriochœrus.* U. Eoc., N. Amer.

† *Agriochœrus.* L. to U. Olig., N. Amer.

† *Oreodon.* L. to M. Olig., N. Amer.

† *Leptauchenia.* M. to U. Olig., N. Amer.

† *Promerycochœrus.* U. Olig. to U. Mioc., N. Amer.

† '*Eporeodon*' (= *Eucrotaphus*). U. Olig., N. Amer.

† *Merychyus.* L. Mioc. to L. Plioc., N. Amer.

† *Mesoreodon.* L. Mioc., N. Amer.

† *Merycochœrus.* L. to M. Mioc., N. Amer.

† *Phenacocœlus.* L. Mioc., N. Amer.

† *Ticholeptus.* M. Mioc., N. Amer.

† *Pronomotherium.* M. to U. Mioc., N. Amer.

† *Cyclopidius.* M. Mioc., N. Amer.

(4) Section *TYLOPODA.* Camels and Llamas.

Fam. **Camelidæ.** Camels and Llamas.

† *Protylopus.* U. Eoc., N. Amer.

† *Oromeryx.* U. Eoc., N. Amer.

† *Eotylopus.* L. Olig., N. Amer.

† *Poëbrotherium.* L. to U. Olig., N. Amer.

† *Pseudolabis.* U. Olig., N. Amer.

† *Oxydactylus.* U. Olig. to L. Mioc., N. Amer.

† *Miolabis.* M. Mioc., N. Amer.

† *Alticamelus.* M. Mioc. to L. Plioc., N. Amer.

† *Protolabis.* M. to U. Mioc., N. Amer.

† *Procamelus.* U. Mioc. to L. Plioc., N. Amer.

† *Pliauchenia.* U. Mioc. to M. Plioc., N. Amer.?; Plioc., India.

† *Camelops.* Pleist., N. Amer.

† *Eschatius.* Pleist., N. Amer.

† *Palæolama.* Pleist., S. Amer.

Camelus. Camel, Dromedary. C. As., N. Afr. (Plioc., As.; Pleist., As., N. Afr., N. Amer.).

Auchenia. Llama, Vicuña. W. S. Amer. (since Plioc.).

Subfam. Stenomylinæ. Stenomylins.

† *Stenomylus.* U. Olig., N. Amer.

(5) Section *TRAGULINA.* Tragulines. Primitive and Ancestral Deer-like Ruminants.

Fam. **Gelocidæ.** Gelocids.

† *Gelocus.* L. Olig., Eur.

† *Bachitherium.* L. Olig., Eur.

† *Prodremotherium.* L. Olig., Eur.

† *Lophiomeryx.* U. Eoc. to L. Olig., Eur.

Fam. **Hypertragulidæ.** Hypertragulids, Primitive Traguloids.

Subfam. Leptotragulinæ. Leptotragulines.

† *Leptotragulus.* U. Eoc., N. Amer.

† *Leptoreodon.* U. Eoc., N. Amer.

SUBFAM. Leptomerycinæ. Leptomerycines or Ancestral Deer.

† *Leptomeryx.* L. to U. Olig., N. Amer.

SUBFAM. Protoceratinæ. Four-horned Traguloids.

† *Protoceras.* U. Olig., N. Amer.

† *Syndyoceras.* U. Olig., N. Amer.

SUBFAM. Hypertragulinæ. Hypertragulines.

† *Hypertragulus.* M. to U. Olig., N. Amer.

SUBFAM. Hypisodontinæ. Hypisodonts.

† *Hypisodus.* M. Olig., N. Amer.

FAM. **Tragulidæ.** Chevrotains.

SUBFAM. Dorcatheriinæ. Dorcatheres or Water Chevrotains.

† *Dorcatherium.* L. to U. Mioc., Eur.; L. Plioc., As.

Hyæmoschus. Water Chevrotain. W. Afr.

SUBFAM. Tragulinæ. Chevrotains Proper.

Tragulus. Chevrotain. India (since L. Plioc.); Siam, Malacca, E. Indies.

(6) SECTION *PECORA.* True or Modernized Ruminants.

FAM. **Giraffidæ.** Giraffes.

† *Palæotragus.* L. Plioc., Eur.

† *Samotherium.* An Extinct Okapi. U. Mioc., Eur.

Ocapia. Okapi. Congo.

† *Helladotherium.* An Extinct Giraffe. L. Plioc., Eur. & As.

† *Sivatherium.* L. Plioc., As.

† *Hydaspitherium.* L. Plioc., As.

† *Vishnutherium.* L. Plioc., As.

Giraffa. Giraffe. E., W. & S. Afr. (L. Plioc., Eur. & As.).

FAM. **Cervidæ.** Deer.

SUBFAM. Palæomerycinæ. Palæomerycines.

† *Blastomeryx.* L. Mioc. to L. Plioc., N. Amer.

† *Palæomeryx.* M. & U. Mioc., Eur.; (?) L. Plioc., India.

† *Dromomeryx.* M. & U. Mioc., N. Amer.

† *Dremotherium.* M. to U. Olig., Eur.

† *Amphitragulus.* M. to U. Olig., Eur.

SUBFAM. Moschinæ. Musk Deer.

Moschus. Musk Deer. C. As., Indo-China (? L. Plioc., India).

SUBFAM. Cervulinæ. Cervulines or Muntjacs.

† *Dicrocerus.* L. to U. Mioc., Eur.

† *Micromeryx*. M. & U. Mioc., Eur.

Cervulus. Muntjac. India, China to Borneo (U. Mioc. & Plioc., Eur.).

Elaphodus. Tufted Deer. Thibet.

Hydropotes. Chinese Water Deer. E. China.

Subfam. Cervinæ. Old and New World Deer, Elk, Moose, etc.

A. Plesiometacarpalia.

Cervus. True Deer, Wapiti, etc. Entire Palæarctic realm. (Since Plioc., Eur.; Pleist., N. Amer.)

Subgenus *Rusa*. Rusine Group.

C. aristotelis, etc. Sambar Deer. India, China, Borneo, etc.

Subgenus *Rucervus*. Rucervine Group.

C. duvauceli, etc. India, Siam, Burma, Hainan.

Subgenus *Elaphurus*. Elaphurine Group.

C. davidianus. David's Deer. China.

Subgenus *Axis*. Axine Group.

C. axis. Axis. India (Plioc., Eur., India).

Subgenus *Pseudaxis*. Pseudaxine or Sicine Group.

C. sika, etc. Sika Deer. China, Japan.

Subgenus *Cervus*. Elaphine Group.

C. elaphus. Red Deer. C. & N. As.; Eur. (since Pleist.).

C. canadensis. Wapiti ('Elk'). N. Amer.

C. maral. Maral. Persia, etc.

† Subgenus *Megaceros*. Megacerotine Group.

† *C. giganteus*. Megaceros, 'Irish Elk.' Pleist., Eur.

Subgenus '*Polycladus*' (=*Eucladocerus*). Polycladine Group.

C. polycladus. Plioc., France.

C. sedgwickii. Plioc., France & Brit.

Subgenus *Dama*. Damine or Fallow Deer Group.

C. dama. Fallow Deer. Eur. (since Pleist.).

C. mesopotamiæ. Persian Fallow Deer. Persia.

C. falconeri, etc. Pleist., Eng.

B. Telemetacarpalia.

Rangifer. Reindeer, Caribou. Circumpolar; (Pleist. Eur., As., N. Amer.).

Alces. Elk, Moose. Scandinavia to Siberia, N. N. Amer. (since Pleist.).

† *Cervalces*. Pleist., N. Amer.

Capreolus. Roe Deer. Eur., W., N. & C. As. (since L. Plioc.).

'*Cariacus*' (= *Odocoileus*). American Deer. N. Amer (since L. Pleist.), C. Amer., W. S. Amer.

'*Pudua*' (= *Mazama*). Pudu Deer, Brocket. S. Amer. to Mexi. (Pleist., S. Amer.).

Fam. **Merycodontidæ**. Merycodonts, with branched deciduous antlers.

† *Merycodus*. M. Mioc. to L. Plioc., N. Amer.

† *Capromeryx*. Pleist., N. Amer.

Fam. **Antilocapridæ**. Pronghorn Antelopes, with forked deciduous horn sheaths and permanent horn cores.

Antilocapra. Pronghorn Antelope. W. N. Amer. (since Pleist.).

Fam. **Bovidæ**. Antelopes, Sheep, Goats, Chamois, Bovines, etc.

Subfam. Tragocerinæ, with flat horns.

† *Protragocerus*. L. to U. Mioc., Eur.

† *Tragocerus*. U. Mioc., Plioc., Eur. & As.

† *Neotragocerus*. L. Plioc., N. Amer.

Subfam. Bubalidinæ. Gnus, Hartebeests, etc.

Bubalis. Hartebeest. Afr., Syria.

Damaliscus. Blessbok, Sassaby, etc. E. & S. Afr.

Connochætes. Wildebeest, Gnu. E. & S. Afr.

Subfam. Cephalophinæ. Duikers, etc.

Cephalophus. Duiker, Afr. (exc. N.).

Tetraceros. Four-horned Antelope. India (since L. Pleist.).

Subfam. Neotraginæ. Dik-dik, Klipspringer, etc. (small forms).

Oreotragus. Klipspringer. S. & E. Afr.

Ourebia. Oribi. E. & S. Afr.

Raphicerus. Steenbok, Grysbok. S., E. & W. Afr.

Nesotragus. Livingstone's Antelope. E. Afr.

Madoqua. Dik-dik. N.E. to S.W. Afr.

Subfam. Cervicaprinæ. Waterbuck, Rhebok, etc. (large forms).

Cobus. Waterbuck. Afr. (exc. N.).

Cervicapra. Reitbok. S. & E. Afr.

Pelea. Rhebok. S.E. Afr.

Subfam. Antilopinæ. Gazelles, Blackbuck, etc.

Antilope. Blackbuck. India.

Gazella. Gazelle. Afr., W. & C. As. (U. Mioc. & Plioc., Eur. & As.).

Antidorcas. Springbuck. S. Afr. (L. Plioc., Eur. & As.).

Saiga. Saiga. S. Russ., W. As. to Altai Mts. (Pleist., Eur.).

Pantholops. Chiru. C. As., Thibet.

Lithocranius. Gerenuk. E. & N.E. Afr.

Æpyceros. Pallah. S. & S.E. Afr.

Subfam. Hippotraginæ. Long-horned Antelopes.

† *Palæoryx.* Plioc., Eur., As.

Hippotragus. Sable Antelope, Roan Antelope. S. & E. Afr.

Oryx. Oryx. Afr. (exc. N.), Arabia.

Addax. Addax. Morocco to Syria.

Subfam. Tragelaphinæ. Eland, Kudu, etc.

† *Palæoreas.* U. Mioc., Eur.; L. Plioc., As.; Plioc., Italy & N. Afr.

† *Protragelaphus.* L. Plioc., Eur. & As.

Boselaphus. Nilgai. India (since Pleist.).

Tragelaphus. Harnessed Antelope. S. Afr. to Congo & to Somali (? Plioc., Eur. & As.).

Strepsiceros. Kudu. S. Afr. to Somali (Plioc., Pleist., Eur., As.).

Oreas. Eland. Afr. (exc. N.).

† *Ilingoceros.* L. Plioc., N. Amer.

† *Sphenophalos.* L. Plioc., N. Amer.

Subfam. Rupicaprinæ. Mountain Goats, Chamois, etc.

Rupicapra. Chamois. Mts. of S. Eur. & S.W. As. (Pleist., Eur.).

Cemas. Goral. C. As., China, E. Siberia.

Nœmorhedus. Serow. C. As. to Sumatra, Japan.

Budorcas. Takin. Thibet, Indo-China.

Haplocerus (=*Oreamnos*). Rocky Mountain Goat. Alaska, Rocky Mts. (Pleist., N. Amer.).

Subfam. Caprinæ. Sheep and Goats.

† *Criotherium.* U. Mioc., Eur.

Capra. Goat, Ibex, Markhor. Mts. of S. & C. Eur., As., N.E. Afr. (Plioc., As.; Pleist., Eur.).

Hemitragus. Tahr. India, Arabia.

Ovis. Bighorn, Mouflon, Sheep. W. N. Amer., As., S. Eur., Egypt.

Subfam. Ovibovinæ. Musk-oxen.

† *Preptoceras.* Pleist., N. Amer.

† *Euceratherium.* Pleist., N. Amer.

† *Symbos.* Pleist., N. Amer.

Ovibos. Musk-ox. Arctic As., Eur., N. Amer. (Pleist., N. Amer. & Eur.).

SUBFAM. Bovinæ. Oxen.

Anoa. Pigmy Buffalo. Celebes.

Bubalus. Cape or African Buffalo, Indian Buffalo. Afr. (exc. N.), W. As. to Borneo (Pleist., N. Afr.).

Bibos. Gayal, Zebu, Gaur. India, Indo-China, East Indies (Plioc., China; Pleist., India).

Poëphagus. Yak. Himalayas, Thibet.

Bos. Domestic Cattle, Urus. Cosmopolitan (domestic). (Plioc. Pleist., As.; Pleist., Eur.)

Bison. American Bison, European Bison or Wisent. Prairies of W. U.S.A., N.W. Canada, Caucasus (Pleist., Eur., N. Amer.).

XVI. ORDER **PERISSODACTYLA.** Odd-toed Ungulates.[1]

SUPERFAM. *HIPPOIDEA.* Horses and Palæotheres.

FAM. **Palæotheriidæ.** Palæotheres.

† (?) *Propachynolophus.* L. Eoc., Eur.

† *Propalæotherium.* M. Eoc., Eur.

† *Palæotherium.* U. Eoc. to L. Olig., Eur.

† *Plagiolophus.* U. Eoc., Eur.

FAM. **Equidæ.** Equines.

SUBFAM. Hyracotheriinæ. Hyracotheres.

† *Hyracotherium.* L. Eoc., Eur.

† *Eohippus.* L. Eoc., N. Amer.

† *Pachynolophus.* M. Eoc., Eur.

† *Lophiotherium.* U. Eoc., Eur.

† *Orohippus.* M. Eoc., N. Amer.

† *Epihippus.* U. Eoc., N. Amer.

SUBFAM. Anchitheriinæ. Anchitheres.

† *Anchilophus.* U. Eoc., Eur.

† *Mesohippus.* L. Olig., N. Amer.

† *Miohippus.* U. Olig., N. Amer.

† *Anchitherium.* U. Olig., N. Amer.; L. to U. Mioc., Eur.

† *Parahippus.* U. Olig. to L. Plioc., N. Amer.

† *Archæohippus.* M. Mioc., N. Amer.

† *Hypohippus.* M. Mioc. to L. Plioc., N. Amer.

[1] For the classification of the Perissodactyla, see Osborn, The Extinct Rhinoceroses, *Mem. Amer. Mus. of Nat. Hist.*, Vol. I, 1898; Weber, Die Säugetiere, 1904. The present arrangement is by Osborn.

Subfam. Protohippinæ. Protohippines, or American Miocene Horses.

† *Merychippus.* M. Mioc. to L. Plioc., N. Amer.

† *Protohippus.* U. Mioc., N. Amer.

† *Pliohippus.* U. Mioc. to L. Plioc., N. Amer.

† *Neohipparion.* U. Mioc. to L. Plioc., N. Amer.

† *Hipparion.* Plioc., Eur., As., N. Amer.

Subfam. Equinæ. Hippidion, Horse, Ass, Zebra.

† *Onohippidion.* Pleist., S. Amer.

† *Hippidion.* Pleist., S. Amer.

Equus. Horse, Ass, Zebra, C., S., & W. As., Afr. (U. Plioc. & Pleist., N. Amer., As., Eur., N. Afr.).

Superfam. *Titanotheroidea.* Titanotheres.

Fam. **Palæosyopidæ.** Palæosyopids.

† *Lambdotherium.* L. Eoc., N. Amer.

† *Eotitanops.* L. Eoc., N. Amer.

† *Palæosyops.* M. Eoc., N. Amer.

† *Telmatherium.* M. & U. Eoc., N. Amer.

† *Manteoceras.* M. & U. Eoc., N. Amer.

† *Mesatirhinus.* M. Eoc., N. Amer.

† *Metarhinus.* U. Eoc., N. Amer.

† *Dolichorhinus.* U. Eoc., N. Amer.

† *Diplacodon.* U. Eoc., N. Amer.

† *Protitanotherium.* U. Eoc., N. Amer.

† *Brachydiastematherium.* U. Eoc., Eur.

Fam. '**Titanotheriidæ**' (= Brontotheriidæ). Brontotheres or Titanotheres.

† *Megacerops.* L. Olig., N. Amer.

† *Titanotherium.* L. Olig., N. Amer.

† *Symborodon.* L. Olig., N. Amer.

† *Brontotherium.* L. Olig., N. Amer.

Superfam. *Tapiroidea.* Tapirs and Lophiodonts.

Fam. **Tapiridæ.** Tapirs.

† *Systemodon.* L. Eoc., N. Amer.

† *Isectolophus.* M. & U. Eoc., N. Amer.

† *Protapirus.* L. Olig., Eur.; M. & U. Olig., N. Amer.

† *Paratapirus.* M. Olig., Eur.

† '*Tapiravus*' *rarus.* M. Mioc., N. Amer.

Tapirus. Tapir. S. Mex. to Paraguay, S. Siam to Sumatra (Plioc., Eur., As.; Pleist. N. Amer.).

Fam. **Lophiodontidæ**. Lophiodonts.

† *Heptodon*. L. Eoc., N. Amer.

† *Lophiaspis*. L. Eoc., Eur.

† *Helaletes*. M. Eoc., N. Amer.

† '*Triplopus*' (*amarorum*). M. Eoc., N. Amer.

† *Desmatotherium*. M. Eoc., N. Amer.

† *Chasmotherium*. M. Eoc., Eur.

† *Lophiodon*. M. to U. Eoc., Eur.

† *Colodon*. L. & M. Olig., N. Amer.

Superfam. *Rhinocerotoidea*. Rhinoceroses and Rhinoceros-like Animals.

Fam. **Hyracodontidæ**. Hyracodonts.

Subfam. Hyrachyinæ. Cursorial Rhinoceroses.

† *Hyrachyus*. M. Eoc., N. Amer.

† *Colonoceras*. M. Eoc., N. Amer.

Subfam. Amynodontinæ. Amynodonts or Semi-Aquatic Rhinoceroses.

† *Amynodon*. U. Eoc., N. Amer.

† *Metamynodon*. L. & M. Olig., N. Amer.

Inc. Sed.

† *Ronzotherium*. L. Olig., Eur.

† *Cadurcotherium*. M. Olig., Eur.

Subfam. Hyracodontinæ. Hyracodonts Proper.

† *Triplopus* (*cubitalis*). M. to U. Eoc., N. Amer.

† *Hyracodon*. L. to U. Olig., N. Amer.

Fam. **Rhinocerotidæ**. True Rhinoceroses.

Subfam. Aceratheriinæ. Aceratheres and Diceratheres.

† *Diceratherium*. M. Olig. to L. Mioc., Eur.; U. Olig. & L. Mioc., N. Amer.

† *Trigonias*. L. Olig., N. Amer.

† *Leptaceratherium*. L. & M. Olig., N. Amer.

† *Aceratherium*. (?) M. Olig. to U. Mioc., Eur.; L. Plioc., As.

† *Cœnopus*. L. to U. Olig. & (?) Mioc., N. Amer.

† *Aphelops*. M. Mioc. to L. Plioc., N. Amer.

† *Peraceras*. U. Mioc., N. Amer.

Subfam. Teleoceratinæ. Teleoceratines.

† *Teleoceras*. L. Mioc., Eur.; M. Mioc. to L. Plioc., N. Amer.

SUBFAM. Rhinocerotinæ. Rhinocerotines.

Rhinoceros. Indian One-horned Rhinoceros. Himalayas to Str. of Malacca, Java. (Plioc., As.)

'*Ceratorhinus*' (= *Dicerorhinus*). Sumatran Two-horned Rhinoceros. Burma to Borneo. (L. Mioc., Eur.)

'*Atelodus*' (= *Diceros*). African Two-horned Rhinoceros. E. & S. Afr. (U. Mioc., Eur.)

SUBFAM. Elasmotheriinæ. Elasmotheres.

† *Elasmotherium.* Pleist., Eur. & As.

XVII. ORDER **ANCYLOPODA.** Ancylopods.[1]

FAM. **Chalicotheriidæ.** Chalicotheres.

† *Pernatherium.* U. Eoc., Eur.

† *Schizotherium.* M. Olig., Eur.

† *Moropus.* U. Olig. to U. Mioc., N. Amer.

† *Macrotherium.* U. Olig. to M. Mioc., Eur.

† *Chalicotherium.* U. Mioc. to L. Plioc., Eur. & As.

† *Ancylotherium.* L. Plioc., Eur.

XVIII. ORDER **PROBOSCIDEA.** Proboscideans.[2]

FAM. **Mœritheriidæ.** Mœritheres.

† *Mœritherium.* U. Eoc. & L. Olig., N. Afr.

FAM. **Elephantidæ.** Dinotheres, Mastodons, and Elephants.

SUBFAM. Dinotheriinæ. Dinotheres.

† *Dinotherium.* L. Mioc. to Plioc., Eur.; L. Plioc., As.

SUBFAM. Mastodontinæ. Mastodons.

† *Palæomastodon.* L. Olig., Egypt.

† '*Trilophodon*,' '*Tetrabelodon*' (= *Gomphotherium*). L. to U. Mioc., Eur.; Mioc. & Plioc., As.; Plioc., Afr.; M. to U. Mioc., N. Amer.

† '*Tetralophodon*' (= *Dibelodon*). Plioc., As., N. Amer.; Pleist., S. Amer.

† *Mastodon.* Plioc. & Pleist., Eur., As.; Pleist., S. Afr., N. Amer.

SUBFAM. Elephantinæ. Mammoths and True Elephants.

† *Stegodon.* Siwalik Mammoth. Plioc., As.

[1] *Vide* Osborn, The Ancylopoda, etc., *Amer. Natural.*, Vol. XXVII, 1893, pp. 118–133. The Ancylopoda are probably aberrant perissodactyls. See also Peterson, Preliminary Notes on Some American Chalicotheres, *Amer. Natural.*, Vol. XLI, 1907, pp. 733–752.

[2] An excellent review of the evolution of the group is given by Lull, R. S., The Evolution of the Elephant. *Amer. Jour. Sci.*, Vol. XXV, March, 1908. See also Osborn, H. F., Hunting the Ancestral Elephant in the Fayûm Desert, *The Century Magazine*, Vol. LXXIV, October, 1907, pp. 815–835. For the Fayûm genera, *Mœritherium* and *Palæomastodon*, see Andrews, C. W., A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt, *Brit. Mus. Nat. Hist.*, 4to, London, 1906.

Elephas. Asiatic Elephant. India to Malacca, Borneo; Mammoth (Plioc. & Pleist., Afr., Eur., As., N. Amer.).

Loxodonta. African Elephant. Cameroons to Germ. E. Afr.

Inc. Sed.

XIX. Order **BARYTHERIA**. Barytheres.[1]

Fam. **Barytheriidæ**. Barytheres.

† *Barytherium*. L. Olig., N. Afr. (Fayûm).

XX. Order **SIRENIA**. Sirenians (Aquatic modification of the Ungulate type).[2]

Fam. **Halicoridæ**. Halicorids.

† *Prorastomus*. Eoc., W. Indies.

† *Eotherium*. U. Eoc., Egypt.

† *Eosiren*. U. Eoc., Egypt.

† *Halitherium*. Olig. & L. Mioc., Eur.

† *Metaxytherium*. Mioc., Eur.

'*Halicore*' (= *Hydrodamalis*). Dugong. Red Sea, Indian Ocean.

Manatus. Manatee. Rivers of N.E. S. Amer., W. Afr.

† *Rhytina*. Northern Sea Cow (lately extinct). Behring Sea.

Fam. **Desmostylidæ**. Desmostylids.

† *Desmostylus*. Plioc., W. N. Amer., Japan.

XXI. Order **HYRACOIDEA**. Hyraces or Coneys.[3]

Fam. '**Hyracidæ**' (= Procaviidæ). Hyraces.

† *Saghatherium*. L. Olig., Egypt.

† *Megalohyrax*. L. Olig., Egypt.

† *Pliohyrax*. U. Mioc., Eur.

'*Hyrax*' (= *Procavia*). Coney or Dassie. Afr. (exc. N.W.), Syria, Arabia.

Dendrohyrax. Tree Hyrax. Afr. (exc. N.).

XXII. Order **EMBRITHOPODA**. Embrithopods.[4]

Fam. **Arsinoïtheriidæ**. Arsinoïtheres.

† *Arsinoïtherium*. L. Olig., N. Afr.

[1] *Vide* Andrews, C. W., A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. 1906.

[2] *Vide* Weber, Die Säugetiere, 1904. For the supposed relationship of the Sirenia to the Proboscidea, see Andrews, C. W., A Descriptive Catalogue of the Vertebrata of the Fayûm, Egypt, introduction.

[3] *Vide* Weber, Die Säugetiere, 1904.

[4] *Vide* Andrews, C. W., A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. 1906.

SUPERORDER **NOTOÜNGULATA**. Extinct South American Hoofed Mammals.[1]

XXIII. ORDER **TOXODONTIA**. Toxodonts, with rhinoceros-like grinding teeth.

1. SUBORDER **HOMALODOTHERIA**. Homalodotheres.

FAM. **Notostylopidæ**. Notostylopids.

† *Notostylops*. Notostylops Beds (? Bas. Eoc.), S. Amer.

† *Trigonostylops*. Notostylops Beds (? Bas. Eoc.), S. Amer.

FAM. **Homalodotheriidæ**. Homalodotheriids.

† *Homalodotherium*. Santa Cruz Beds (? U. Mioc.), S. Amer.

Inc. Sed.

† *Asmodeus*. Pyrotherium Beds (? Eoc.), S. Amer.

2. SUBORDER **ASTRAPOTHERIA**. Astrapotheres.

Inc. Sed. FAM. **Albertogaudryidæ**. Albertogaudryids.

† *Albertogaudrya*. Notostylops Beds (? Bas. Eoc.), S. Amer.

† (?) *Astraponotus*. Astraponotus Beds (? Bas. Eoc.), S. Amer.

Inc. Sed. FAM. **Isotemnidæ**. Isotemnids.

† *Isotemnus*. Notostylops Beds (? Bas. Eoc.), S. Amer.

FAM. **Astrapotheriidæ**. Astrapotheres.

† *Astrapotherium*. Colpodon Beds (? Mioc), and a type species in Santa Cruz Beds (? U. Mioc.), S. Amer.

3. SUBORDER **TOXODONTIA**. True Toxodonts.

Inc. Sed. FAM. **Archæohyracidæ**. Archæohyracids.

† *Archæohyrax*. Pyrotherium Beds (? U. Eoc.), S. Amer.

† *Rhynchippus*. Pyrotherium Beds (? U. Eoc.), S. Amer.

FAM. **Toxodontidæ**. Toxodontids.

† *Nesodon*. Santa Cruz Formation (? U. Mioc.), S. Amer.

† *Toxodon*. Pampean (? Plioc. & Pleist.), S. Amer.

† *Colpodon*. Colpodon Beds (? Mioc.), S. Amer.

4. SUBORDER **TYPOTHERIA**. Typotheres.

FAM. **Interatheriidæ**. Interatheres.

† *Protypotherium*. Santa Cruz (? U. Mioc.), S. Amer.

[1] *Vide* Weber, Die Säugetiere, 1904 (under 'Litopterna, Toxodontia,' etc.); A. Smith Woodward, Outlines of Vertebrate Palæontology, Cambridge, 1898; Von Zittel, Paläontologie, IV Bd., Mammalia. Among the numerous monographic researches by Ameghino, Lydekker, Roth, Gaudry, Scott, Sinclair, may be mentioned especially: Lydekker's A Study of the Extinct Ungulates of Argentina, *Paleontologia Argentina*, II, *An. del Museo de la Plata*, 1893; the monographs (now in press) by Professor Scott and Dr. Sinclair in the Princeton Univ. Exped. to Patagonia; Sinclair's article, The Santa Cruz Typotheria, *Proc. Amer. Philos. Soc.*, Vol. XLVII, 1908, pp. 64–78; and Gaudry's memoirs in the *Annales de Paléontologie* (Marcellin Boule), 1906–1909. The present provisional arrangement is by Gregory.

† *Interatherium*. Santa Cruz (? U. Mioc.), S. Amer.

Fam. **Hegetotheriidæ**. Hegetotheres.

† *Hegetotherium*. Santa Cruz (? U. Mioc.), S. Amer.

† *Pachyrukhos*. Santa Cruz (? U. Mioc.), S. Amer.

Fam. **Typotheriidæ**. Typotheriids.

† *Typotherium*. Pampean (? Plioc. & Pleist.), S. Amer.

XXIV. Order **LITOPTERNA**. Litopterns, with palæothere- and horse-like grinding teeth.

Fam. **Proterotheriidæ**. Proterotheres.

† *Proterotherium*. Santa Cruz (? U. Mioc.), S. Amer.

† *Diadiaphorus*. Santa Cruz (? U. Mioc.), S. Amer.

† *Thoatherium*. Santa Cruz (? U. Mioc.), S. Amer.

Fam. **Macraucheniidæ**. Macrauchenids.

† *Theosodon*. Santa Cruz (? U. Mioc.), S. Amer.

† *Scalabrinitherium*. Pampean (? Plioc. & Pleist.), S. Amer.

† *Macrauchenia*. Pampean (? Plioc. & Pleist.), S. Amer.

XXV. Order **PYROTHERIA**. Pyrotheres, Mastodon-like South American Ungulates.[1]

Fam. **Pyrotheriidæ**. Pyrotheres.

† *Carolozittelia*. Notostylops Beds (? Bas. Eoc.), S. Amer.

† *Propyrotherium*. Pyrotherium Beds (? U. Eoc.), S. Amer.

† *Pyrotherium*. Pyrotherium Beds (? U. Eoc.), S. Amer.

d. Cohort CETACEA. Whales and Dolphins.[2]

XXVI. Order **ZEUGLODONTIA** (Archæoceti). Archaic Cetaceans.

Fam. '**Zeuglodontidæ**' (= Basilosauridæ). Zeuglodons.

† *Protocetus*. U. Eoc., N. Afr.

† *Prozeuglodon*. U. Eoc., N. Afr.

† '*Zeuglodon*' (= *Basilosaurus*). U. Eoc., N. Amer., Eur., N. Afr.; Tertiary, New Zealand.

XXVII. Order '**ODONTOCETI**' (= Denticeti). Toothed Whales.

Fam. **Squalodontidæ**. Squalodonts.

† *Squalodon*. U. Eoc., N. Amer.; Mioc., Eur., Austral.

† *Prosqualodon*. Mioc., S. Amer.

[1] *Vide* Gaudry, A., Fossiles de Patagonie: Le Pyrotherium, *Ann. de Paléontologie* (Marcellin Boule), tome IV, 1909; for review and summary of this, see Gregory, W. K., in *Science*, n.s., Vol. XXX, 1909, pp. 180–182.

[2] *Vide* Weber, Die Säugetiere, 1904; Beddard, F. E., The Book of Whales, New York, 1900; and Beddard in Cambridge Natural History, volume Mammals; Flower and Lydekker, Introduction to the Study of Mammals, 1891.

FAM. **Argyrocetidæ**. Argyrocetids.

† *Argyrocetus*. U. Mioc., S. Amer.

FAM. **Platanistidæ**. River Dolphins.

Platanista. Susu, Ganges Dolphin. Rivers of India, Burma, Assam.

Inia. Inia, Amazon Dolphin. Amazon, Orinoco, etc.

Stenodelphis. La Plata Dolphin. La Plata, Rio Grande do Sul.

FAM. **Delphinidæ**. Dolphins, Porpoises, Killers, etc.

Sotalia. White River Dolphin. Ind. Oc., W. Afr., Guiana, Brazil.

Steno. Rough-toothed Dolphin. Atlant., Pacif., Ind. Oc.

Tursiops. Bottle-nosed Dolphin. Pacif., Atlant., Medit. & Red Sea, Ind. Oc.

Delphinus. Dolphin. Cosmopolitan in Oceans.

Lagenorhynchus. Spectacled Dolphin. Atlant. & Pacif. (N. & S.), Ind. Oc.

Phocæna. Porpoise. Atlant. & Pacif. (N. & S.), Medit. Sea.

Orcella. Orcella, Irawadi Dolphin. Rivers of Bengal, Burma, Borneo.

Grampus. Grampus. N. Atlant., Pacif., Ind. Oc., Medit. Sea.

Globicephalus. Ca'ing 'Whale,' Blackfish. Atlant., Pacif., Ind. Oc., Medit. Sea.

Pseudorca. Lesser Killer. Cosmopolitan in Oceans.

Orca. Killer 'Whale.' Cosmopolitan in Oceans.

FAM. **Delphinapteridæ**. Belugas and Narwhals.

Delphinapterus. Beluga. Arctic, Atlant., N. Pacif. Oc.

Monodon. Narwhal. Arctic, N. Atlant. (W.) Oc.

FAM. **Physeteridæ**. Sperm Whales and Beaked Whales.

SUBFAM. Physeterinæ. Sperm Whales.

† *Physodon*. U. Eoc., S. Amer.; Mioc., Eur.

Physeter. Sperm Whale. Atlant., Pacif., Ind. Oc.

Cogia. Pygmy Sperm Whale. Pacif., Ind., S. Atlant. Oc.

SUBFAM. Ziphiinæ. Beaked Whales.

Hyperoödon. Bottle-nose Whale. N. Atlant., Medit. Sea, S. Pacif., Antarctic Oc. (Plioc., Eur.).

Ziphius. Two-toothed Whale. Cosmopolitan in Oceans.

Mesoplodon. Cow Fish. Atlant., Pacif., Ind. Oc. (Plioc. Eur.; Pleist., N. Amer.).

Berardius. New Zealand Two-toothed Whale. S. Pac. Oc. near N. Zealand.

XXVIII. Order **MYSTACOCETI**. Whalebone Whales.

Fam. **Balænidæ**. Whalebone Whales.

Subfam. Rhachianectinæ. Gray Whales.

Rhachianectes. Gray Whale. N. Pacif. Oc.

Subfam. Balænopterinæ. Rorquals.

† (?) *Plesiocetus*. Mioc. & Plioc., Eur.

† (?) *Cetotherium*. Mioc., Eur. & N. Amer.

Balænoptera. Rorqual, Fin Whale, etc. Cosmopolitan in Oceans. (Plioc., Eur.)

Megaptera. Hump-backed Whale. Cosmopolitan in Oceans. (Plioc., Eur.)

Subfam. Balæninæ. Right Whales.

Balæna. Right Whale. Arctic, N. Pacif., N. Atlant. Oc.

Neobalæna. Pygmy Right Whale. S. Pacif. Oc. (Austral. to Chili).

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